University of Alberta

The effects of habitat composition and configuration on the behaviour and reproductive success of Northern Saw-whet Owls

by

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Abstract

Studies of habitat fragmentation have been heavily biased toward population and community effects, with less attention to the effects of habitat on individual behaviour and reproduction. Yet, understanding fitness effects on individuals can both explain and mitigate population effects. I studied the effects of habitat composition and configuration on the behaviour and fitness of northern saw-whet owls (*Aegolius acadicus*) in the fragmented aspen parkland of central Alberta, Canada. Specifically, I examined the effects of forest fragmentation on 1) the foraging and provisioning behaviour and reproductive success of breeding males, 2) the growth, condition and survival of developing nestlings and 3) the behaviour, condition and survival of fledgelings. Adult males breeding in areas with less forest cover and larger inter-patch distances spent more time perching, maintained smaller home ranges, and provisioned their nests less frequently. These males, and those raising large broods, also exhibited higher heterophil:lymphocyte (H:L) ratios, indicating higher levels of chronic stress. Predictably, males that provisioned the nest less often fledged fewer young, which, in turn, varied widely in physiological condition. In more general terms, owls nesting in areas with less forest cover and more fragmented landscapes raised nestlings that grew at a slower rate and had greater within-nest variation in both residual mass and H:L ratios. In addition, saw-whets nesting in landscapes with less forest cover were more likely to lose at least one nestling to brood reduction and thus fledged fewer young. Juveniles that fledged in more fragmented landscapes stayed closer to their nests post-fledging and remained longer in the natal territory before dispersal. In addition, juveniles in more forested landscapes had lower residual mass and exhibited a decline during the first month post-fledging in chronic stress, as measured by H:L ratios. Lastly, juveniles in more forested landscapes and those that fledged with low H:L ratios were more likely to survive the first month post-fledging. This study has demonstrated measurable effects of habitat loss and fragmentation on individual behaviour and fitness, providing a mechanistic basis to aid in the understanding of the larger effects of habitat composition and configuration on population viability.

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Chapter 1 – Introduction to the Thesis

The effects of habitat loss and fragmentation on organisms have been topics of intense study for about 30 years, generating hundreds of papers (see Fahrig 2003; Cushman 2006; Ewers and Didham 2006; for reviews). Habitat loss has been identified as a pervasive cause of population declines (e.g. Gibbs 1998; Donovan and Flather, 2002; Reed 2004) and species loss (e.g. Wettstein and Schmid 1999; Schmiegelow and Mönkkönen 2002; Brooks et al. 2002) across numerous taxa, from insects (Wettstein and Schmid 1999) and amphibians (Gibbs 1998; Cushman 2006) to birds (Schmiegelow and Mönkkönen 2002; Betts et al. 2006) and mammals (Silva et al. 2005). However, the effect of habitat fragmentation, defined as the subdivision and alteration in the spatial arrangement of remaining habitat patches (*sensu* McGarigal and Cushman 2002), on population numbers has been less clear (Fahrig 2003; Ewers and Didham 2006) and difficult to separate from the concomitant effects of habitat loss (Fahrig 2003). Relationships between increasing habitat fragmentation and measures of population abundance range from positive (e.g McGarigal and McComb 1995; Hovel and Lipcius 2001; Price et al. 2005) and negative (e.g. Rosenburg et al. 1999; Betts et al. 2006) to no effect (e.g. Krauss et al. 2003; Betts et al. 2006). The effects of habitat fragmentation may also vary between species (Wiegand et al. 2005; Betts et al. 2006) and even within a species (Hovel and Lipicius 2001; Wilder and Meikel 2005). These observed patterns concerning populations and communities are generated by often-complex interactions between individuals and their surroundings (Bélisle 2005). Identifying these interactions and their associated demographic responses would aid in understanding the variation in the effects of habitat loss and especially fragmentation on populations and communities

(Yahner and Mahan 1997; Lampila et al. 2005), yet there has been less attention to the effects of habitat change on individuals.

Understanding how habitat loss and fragmentation affect individual fitness is a necessary step in explaining the effects of habitat loss and fragmentation on populations and communities (Lima and Zollner 1996; Yahner and Mahan 1997). This may be achieved by integrating measures of behaviour and physiology into conservation studies (Sutherland 1998; Wikelski and Cook 2006). However, there are relatively few studies that assess the relationships among habitat fragmentation, individual behaviour, condition and fitness. A recent review of over one hundred fragmentation studies identified only fifteen that related habitat to individual fitness and fewer than nine of these addressed individual behaviour (Fahrig 2003). This rarity is surprising because habitat loss and fragmentation may affect individual fitness in at least three ways by: 1) altering individual behaviour, which may affect survival, 2) affecting reproductive output and 3) influencing individual physiological condition, which may affect current or future survival and reproduction.

Habitat loss and fragmentation may influence individual behaviour mainly through their effects on animal movement. Until recently, the effect of habitat on individual movement has been examined largely in the context of one-time dispersal movements from a single habitat patch (e.g. Brooker et al., 1999; Bélisle and Desrochers, 2002; Lin et al. 2006) or by measuring manipulated movement (e.g., Gobeil and Villard 2002; Castellon and Sieving 2006). However, this focus on single movement events and manipulated behaviour may miss important long-term or cumulative effects of fragmentation on individuals. Such effects are most likely for species that occupy multiple habitat patches prior to or beyond the dispersal phase (Grubb and Doherty 1999, Hinsley 2000; Harris and Reed 2002) because the effects of habitat fragmentation are experienced multiple times within an hour, day or season. Crossing barriers between habitat patches on a regular basis throughout a lifetime may compound the effects of habitat loss and fragmentation, through increased physiological costs (Villafuerte et al. 1998; Hinsley 2000; Bélisle and Desrochers, 2002) and higher risk of predation (Lima and Dill, 1990; Andreassen and Ims 1998; Nonacs, 2001). By altering behaviour and reducing physiological condition during important life stages, such as foraging, provisioning young or early independence, these effects of fragmentation may reduce an individual's fitness through lower survival or reproductive success, and ultimately limit population viability (Rolstad, 1991; Hinsley 2000).

The effect of habitat loss and fragmentation on reproductive success has been extensively studied in the context of birds, particularly for open-cup nesting passerines for which lower nest success is associated with higher rates of brood parasitism and predation (see Stevens *et al.* 2003 for review). However, for cavity nesters and raptors, the effects of habitat fragmentation on nest success range from negative (Hakkarainen et al. 2003; Mazgajsk and Reijt 2006) to no effect (Matthysen and Adriaensen 1998). For those species that experience low levels of nest predation, reproductive success appears to be limited mainly by the accessibility of resources and the efficiency with which parents provision young (Mazgajsk and Reijt 2006). Limited resources, in turn, appear to lower reproductive success through smaller clutch sizes (Mazgajsk and Reijt 2006), poorer body condition (Loman 2003) and lower survival rates of the young (Møller 1991; Hinsley, et al. 1999; Hakkarainen et al. 2003; Mazgajsk and Reijt 2006).

Although most avian studies suggest that habitat fragmentation can limit reproductive success in some way, they may underestimate those effects because they typically do not extend to the post-fledging period, when young birds may be vulnerable to several other habitat-induced effects (e.g. Naef-Daenzer et al. 2001; Kershner et al. 2004; Robinson et al. 2004). Once the young leave the nest, the effects of habitat loss and fragmentation on nest success may be compounded by greater predation risk and thus lower survival of juveniles (e.g. Anders et al. 1997; Naef-Daenzer et al. 2001; King et al. 2006), further reducing individual fitness. For these reasons, it is important to study birds throughout the period of juvenile dependence, from laying through to post-fledging dispersal.

An additional mechanism by which habitat loss and fragmentation may affect an individual's fitness is through an increase in chronic stress. This effect too, has received relatively little study, yet it has important implications for populations (Wikelski and Cooke 2006). Habitat loss and isolation of remaining patches may increase the physiological cost of obtaining resources (Villafuerte et al. 1998; Ruiz et al., 2002) and increase predation risk (Navarro et al., 2004; Perez-Tris et al., 2004) resulting in the perception of a more stressful environment. Individuals may respond to stressful environments through a decrease in body condition (Villafuerte et al. 1998;

Perez-Tris et al. 2004) and through repeated spikes of blood corticosterone, leading to immunosuppression (Hõrak et al., 1998; Clinchy et al., 2002). Many studies have found a reduction in potential fitness in individuals experiencing chronic physiological stress through lower probabilities of future survival (Saino et al., 1997) and lower future reproductive success (Hanssen et al., 2003; Boonstra 2004; Hanssen et al., 2005). Understanding the ubiquity of these effects and identifying reliable methods for measuring stress responses could lend much to the study of individual responses to habitat fragmentation.

One reason that there have not been more studies of animal behaviour and physiology in the context of fragmentation is that it is typically logistically difficult (Hames et al. 2001; Wikelski and Cooke 2006). Most studies have been restricted to patch-scale approaches, despite the regional scale of the problem of habitat loss and fragmentation (McGarigal and Cushman 2002; Fahrig 2003).

Forest-dwelling raptors provide an opportunity for examining how habitat loss and fragmentation affect these mechanisms because their large home ranges often encompass multiple habitat patches of forest, interspersed within an often inhospitable matrix (Kirk and Hyslop 1998). One species with the potential for exhibiting behavioural and physiological effects of habitat fragmentation is the highly forest-dependent northern saw-whet owl (*Aegolius acadicus*, Cannings 1993). Partly because of its potential vulnerability to forest loss, a nest box program for this species was established in central Alberta in the early 1980s (R. Cromie, pers comm.). This region is located in the transitional zone of the boreal forest of east-central Alberta, where continuous forest grades into naturally patchy aspen parkland. Much of the landscape has been cleared, leaving a matrix of agricultural and developed land. This configuration would be expected to pose barriers for the movement of forest-dependent species and should also result in a stressful environment. The nest box population offered the opportunity to examine the processes through which habitat loss and fragmentation may affect a species through measurable links to individual behaviour, reproductive success, condition, and thus fitness, and ultimately population viability.

The objective of this thesis was to examine the effects of habitat composition and configuration on the behaviour, reproductive success and physiological condition of the northern saw-whet owl in east-central Alberta. I addressed these objectives by focusing on three aspects of the reproductive behaviour of saw-whet owls: 1) adult foraging and provisioning 2) nestling growth, condition and survival and 3) the behaviour, condition and survival of juveniles during the post-fledging period. These foci produced the three data chapters that follow. The objectives of chapter one were to examine how habitat composition and configuration affected the foraging decisions, home range size and provisioning rates of adult male saw-whet owls, then in turn, the relationship between male provisioning and juvenile condition and nest success. In the second chapter, I asked how habitat composition and configuration affected chick growth, condition, and nest success. In Chapter three, I examined the relationship between habitat loss and fragmentation and juvenile post-fledging movements, physiological condition and survival.

With these three chapters, I set out to identify measurable links between landscape-level habitat loss and fragmentation, individual behaviour and ultimately fitness, through a systematic examination of the effects of habitat variation at each step in the reproductive biology of northern saw-whet owls. The results of this thesis identify components of habitat loss and fragmentation important to individual behaviour and reproductive success. This thesis will also expand our understanding of the mechanisms governing the habitat-mediated variation in avian reproductive success into a species that occupies multiple habitat patches. Finally, I endeavoured to aid in the larger understanding of the effects of habitat loss and fragmentation on patterns of population persistence and community structure by identifying mechanisms through which landscape variation can affect demographics.

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Chapter 2 - Habitat loss and fragmentation limit reproductive success by reducing provisioning rates of Northern Saw-whet Owls.

Introduction

Living in fragmented areas can be costly. In the context of habitats, fragmentation is often used to describe two different, but linked processes: a reduction in the amount of habitat (composition) and changes in the configuration of the remaining patches (Wiens, 1994). The relative influences of habitat composition and configuration have been difficult to separate (Andrèn, 1994; Fahrig, 1997; Villard et al., 1999; Bélisle et al., 2001), and attract ongoing attention (Schmiegelow and Mönkkönen, 2002; Fahrig, 2003; Cushman, 2006). Theoretical work suggests that habitat configuration is often important only below some threshold of habitat amount (With and Crist, 1995; Fahrig, 2003). However, the majority of studies of the effects of loss and fragmentation on habitat quality have focussed mainly on population (e.g. Rolstad, 1991; Bender et al., 1998; Donovan and Flather, 2002) and community responses (e.g. Stouffer and Bierregard, 1995; Schmiegelow et al., 1997; Barlow et al., 2006). In many systems, increasing habitat loss has a consistent negative effect on biodiversity (e.g. Gibbs, 2001; Schmiegelow and Mönkkönen, 2002; see Fahrig, 2003 for review). These habitat changes typically attend declines in population sizes as well (e.g. Rolstad, 1991, Bender et al., 1998; Donovan and Flather, 2002), providing a mechanism for the community responses. However, although several studies have examined the effects of habitat variation on reproductive success (see Stevens et al. 2003 for review), how the behaviour of individuals drives these patterns is still relatively poorly understood.

Recent work on birds has shown that habitat loss increases movement costs to individuals, (Bélisle et al., 2001; Ruiz et al., 2002) and decreases breeding success (Hinsley et al., 1999). Although these effects have received the most attention in the context of individuals occupying a single patch (e.g. Matthysen and Curie, 1998; Brooker et al., 1999; Bélisle and Desrochers, 2002), the effects of habitat loss and fragmentation can also apply to species that maintain home ranges that encompass multiple patches. These individuals may actually be the ones that are more vulnerable to fragmentation effects (Grubb and Doherty, 1999; Hinsley, 2000). For individuals maintaining multiple patch home ranges, smaller and more isolated patches of habitat may require that they consistently travel farther for resources. Indeed, use of multiples patches of habitat within a home range appears to convey substantial costs for several bird species (Redpath,1995b; Hinsley et al., 1999). These costs may accrue from increased energy expenditure to detour around gaps in habitat (e.g. St. Clair et al., 1998; Bélisle and Desrochers, 2002), and higher predation risk (Lima and Dill, 1990; Nonacs, 2001, Redpath, 1995b; Siffczyk et al., 2003, Turcotte and Desrochers, 2003), both of which may lower foraging efficiency and increase physiological costs as a result of chronic stress (Ruiz et al., 2002, Turcotte and Desrocher, 2003). When chronic impediments to movement are associated with critical life stages, such as provisioning young, habitat fragmentation is more likely to reduce the reproductive success of individuals and, potentially, population viability (Rolstad, 1991, Hinsley, 2000).

The northern saw-whet owl (*Aegolius acadicus*) provides an excellent opportunity for examining how habitat fragmentation affects the movements, foraging efficiency and reproductive success of a species occupying multiple habitat patches. These owls are considered to be forest specialists (Cannings, 1993) and thus, generally may be more vulnerable to the effects of habitat fragmentation (Harris and Reed, 2002) because they cannot exploit the surrounding matrix, or moving through the matrix may be too risky (Turcotte and Desrochers, 2003). Although the species can hunt from forest edges, habitat loss and fragmentation likely reduces perch availability and increases exposure of owls to predation from open-area species such as the great horned owl (*Bubo virginianus;* Cannings, 1993). Because males are the sole provisioners to the nest for the bulk of the egg and nestling period (Cannings, 1993), northern saw-whet owls present a relatively simple system for studying foraging and provisioning behaviour and their ultimate effect on reproductive success in the face of varying degrees of forest fragmentation.

Optimal foraging theory (*sensu* Stephens and Krebs, 1986) offers some explicit predictions for how owls foraging in multiple patches might behave in a fragmented landscape. For example, the Marginal Value Theorem suggests that individuals that travel farther between successive patches will spend longer foraging within a given patch (*sensu* Charnov, 1976). As increasing habitat loss and fragmentation isolates resources into patches (Bruun and Smith 2003), individuals may also be obliged to forage farther from their nests (Frey-Roos et al., 1995; Bruun and Smith, 2003), and maintain larger home ranges (Redpath 1995b), resulting in fewer provisioning trips to the nest (Frey-Roos et al., 1995; Bruun and Smith, 2003). Conversely, landscapes may contain so little habitat that the distance between patches may exceed a species' gap-crossing tolerance (e.g., Desrochers and Hannon, 1997; Harris and Reed, 2002). In this case, territorial movements may be constrained to reduce the size of home ranges. Either effect should ultimately reduce the rate at which individuals can provision their young (Frey-Roos et al., 1995; Tella et al., 1998; Hinsley, 2000, Bruun and Smith, 2003) with consequential effects on their own or their offspring's growth and condition (Tarlow et al., 2001). Travelling through fragmented areas may also result in increased stress to the male as a result of increased predation risk (Lima and Dill 1990) and higher movement costs (Hinsley 2000), which may be expressed physiologically (Bélisle et al., 2001; Ruiz et al., 2002) as a decrease in body mass relative to size (Perez-Tris et al., 2004) or in an immunological response (Ruiz et al., 2002).

The objective of this study was to examine how variation in habitat composition and configuration affects the foraging decisions, provisioning behaviour and physiological condition of male northern saw-whet owls. We then examined how male provisioning behaviour, in turn, relates to individual reproductive success and juvenile condition prior to fledging. These objectives, combined with the theory described above, supported five specific predictions. (1) As the distance between patches increases, the time an individual spends in each patch should increase. (2) Male home range size and foraging radius would vary quadratically, increasing as lower forest cover and increasing distance between patches spreads out resources, but then decreasing when the distance between patches becomes greater than individuals are willing to cross. (3)

A reduction in forest cover and an increase in the distance between remaining patches would be reflected in lower provisioning rates. (4) Males that provision the nest less frequently would fledge fewer young and fledglings in poorer physiological condition. (5) Males breeding in areas with low forest cover and greater distances between remaining patches would exhibit poorer physiological condition.

Methods

Study area and species

Field data were collected between 2002 and 2005 in the transition zone between the boreal forest and the aspen parkland north and east of Edmonton, Alberta, Canada (53°32'N, 113°33'W). In this 3,040 sq km study area, approximately 250 nest boxes have been erected since 1985 to support a long-term monitoring project for Northern Saw-whet Owls (R. Cromie pers. comm.). This region is characterized by predominantly flat terrain with a patchy distribution of mature mixedwood forest, interspersed with cropland, pasture and human development. Forest patches are dominated by trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) mixed with white and black spruce (*Picea glauca, P. banksiana*). Nest boxes occurred in a wide variety of forest compositions and configurations. Landscapes within 800 m of nests ranged from 10 to 85 percent forest cover. The mean patch size of these 800 m landscapes ranged from 3.6 to 286 m^2 and the mean edge to edge nearest neighbour distance between patches ranged from 15.3 to 122.2 metres.

The northern saw-whet owl is a small, forest-dwelling, nocturnal species. Breeding males and females in this study area had a mean body mass of 79.8 ± 5.4 (SD) g and 125.1 ± 15.2 g respectively at the point during the season at which young were hatching (Hinam, unpublished data). Saw-whet owls feed mainly on small mammals (Cannings, 1993) and hunt from low perches employing a perch and pounce style of predation (Cannings, 1993).

Home range and foraging behaviour of adult males

Home range size and foraging behaviour were determined by tracking breeding males using radio telemetry. Individuals were captured during or within a week of the hatching period while provisioning their nests using a box trap placed over the entrance to the nest box (Saurola, 1987). This period ranged from early May to mid-July depending on when the nest was initiated. This trap design blocks the female and young inside the box and a trap-door is triggered when the male arrives with food. Because wariness appeared to decrease once the eggs had hatched (H. Hinam, personal observation), males were trapped as soon after hatching as possible. Traps were deployed prior to sunset and left on the nest box until the male was caught or two hours after sunset.

Once captured, males were banded with U.S. Fish and Wildlife Service bands and fitted with backpack PD-2P transmitters (Holohil) using a harness made of Teflon strapping and lightweight polyester material. The transmitter was placed on the back between the scapulae and the straps passed over the shoulders, crossing in an x over the breast before being reattached to the transmitter at the back. After release, males were given a minimum of five days to acclimate to the transmitter and then were tracked for a minimum of three focal bouts during the chick-rearing period. Each focal bout began after sunset and lasted a minimum of three hours. Within this period, two stationary observers continuously and simultaneously monitored an individual owl using hand-held VHF receivers to record all movements between perches and to and from the nest (after Redpath, 1995a, Graham, 2001). Position sensors in the transmitters alerted us to each movement and simultaneous bearings were taken once the individual had settled on a perch. A combination of triangulated and observed locations during these focal periods was used to calculate the distance between successive perches, time spent at each perch, and the maximum radius from the nest of each foraging bout.

We estimated telemetry error using a sub-sample of telemetry fixes on roosting birds, that we then sighted immediately by walking in on them. We calculated mean linear error, standard deviation (SD) of bearing deviations and tested for directional bias in bearing error using a one-sample t-test, testing for a significant deviation from zero degrees (after White and Garrott, 1990).

Home range size was estimated from all position fixes during focal bouts and at daytime roosts during the breeding season using a fixed kernel estimator (Seaman and Powell, 1996) and the Home Range Extension for ArcView GIS (Rodgers and Carr, 2001). Although kernel estimators of home range size assume statistical independence between position fixes (Swihart and Slade 1997), a number of studies have found little difference in home range size estimated using statistically independent locations and those estimated using autocorrelated data (Andersen and Wrongstad 1989; Gese et al. 1990; Reynolds and Landré1990). Thus, it is likely that home range estimates based on autocorrelated data are valid provided fixes are collected over the entire timeframe of interest (Kernohan et al. 2001). In this study, we used groups of autocorrelated fixes from temporally independent focal bouts as well as independent daytime roost sites over the course of the entire nestling season in order to describe the home range use of saw-whets while retaining important data regarding individual movement (Kernohan et al. 2001). Bandwidth (smoothing parameter) was calculated using the least squares cross validation method (Seaman and Powell, 1996). Because the value for this method is dependent on home range size and number of fixes (Kenward, 2001), which ranged from 30 to 75 per individual, we first calculated a smoothing parameter for each male's set of positions individually and then calculated the median of these values. Finally, we recalculated home range size for each male using the median value as the smoothing parameter to allow for comparison among males (Kenward, 2001).

Blood sampling

Male physiological condition was assessed in 2004 and 2005 using the residuals generated from a regression of body mass against tarsus length (Ots et al. 1998) and the ratio of white blood cells, specifically heterophils to lymphocytes (H:L) ratios. This ratio has been identified as a reliable indicator of a bird's response to chronic stress, increasing as stress increases (Gross and Siegel, 1983, Hõrak, 2002) and appearing to be less affected by short-term handling stress than corticosterone levels (Gross and Siegel 1983). Blood samples were taken upon capture by puncturing the ailar vein using a 27 ½ gauge needle and collecting less than one cc of blood in a heparinized capillary tube. One to two whole blood smears per bird were made using a 2-slide wedge method on site (Campbell 1988) and then stored for examination at a later date. Smears were stained within four months of preparation using a Wright stain, buffered using a 2 % solution of Giemsa stain in deionized water (Sigma). We then performed leukocyte differential, classifying a random count of 100 white blood cells into each of five cell types: heterophils, lymphocytes, monocytes, eosinophils and basophils (*sensu* Gross and Siegel 1983). The ratio of heterophils to lymphocytes was calculated from the number of each cell type in that count (Gross and Siegel 1983).

Provisioning Rates

Provisioning rates were measured using an automated weighing system installed in occupied nest boxes. Each scale consisted of a weighing platform inserted into the base of the nest box and connected to an external controller. The device measured and logged the relative mass of the box contents at one-minute intervals on a removable memory module and thus could record when a food load was added to the nest in a provisioning event. We recorded provisioning rates for each nest as the number of food deliveries each night. We did not use mass of prey deliveries as our measure of provisioning rate because the accumulating pad of pellets regurgitated by the developing young reduced the accuracy of our measures of prey masses during the later nestling period. We defined night as the period between sunset (as recorded by Environment Canada at Edmonton, Alberta) and one half hour after sunrise. The scales recorded a food delivery as a sudden change in the scale reading that resulted in a net increase in mass of 10 g or more within the box. We used a 10 g cut off because it the smallest mass that we could discern reliably from background variation in the scale data that would encompass the greatest number of prey types that the owls consume. Deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*), the primary prey of saw-whets in this study area and elsewhere (Cannings, 1993) range between 10 and 40g (Burt and Grossenheider, 1980).

Reproductive success and juvenile condition

Each nest was monitored every two to seven days from the day of discovery until the last of the young fledged, approximately 30 days after hatching. Because most nests fledged at least one juvenile (75 of 78 nests monitored for the entire study period), we used the number of owlets present in the nest just prior to fledging as a measure of reproductive success. We assessed juvenile condition with H:L ratios measured from whole blood smears as for males. Blood samples were taken from the nestlings that were still in the nest just prior to fledging, when the oldest in the nest was approximately 30 days old. We used both the mean H:L ratio of each nest and the standard deviation of H:L ratios (H:L SD) within each nest as measures of juvenile pre-fledging condition. The latter was used because saw-whet young hatch asynchronously

(Cannings, 1993) and it is possible that physiological stress may be manifested not only by higher H:L ratios for the whole nest; but also by a greater difference in H:L ratios between older and younger nestlings (Blas et al., 2005). To account for any potential effects of crowding in the nest on juvenile condition, we included brood size as a factor in the analysis.

Habitat composition, configuration and prey density

We compared the dependent variables of male home range, perch time, H:L ratios and provisioning rates to a set of continuous habitat composition and configuration metrics that were calculated for landscapes centred on each nest. We defined the landscape size as a radius of 800 m radius from the nest. This radius was based on the mean foraging distance from the nest of the males followed during this study ($n = 14$). We overlaid each nest-centred landscape on a GIS forest layer of the study area. This layer was created by enhancing black and white Indian Remote Sensing (IRS) data with a false-colour LANDSAT layer from 1998 and digitizing it into a binary layer of habitat (forest) and non-habitat (all other types). The minimum mapping unit of the LANDSAT data was 30 m^2. However, the 4-m^2 resolution of the IRS layer allowed us to identify fine-scale habitat features such as small woodlots. Based on their perceived importance to owl behaviour and condition, we selected three nest patch metrics, one landscape composition metric, and five landscape configuration metrics to describe each nest-centred landscape. Patch metrics included nest patch size and nest patch shape index, which describes the complexity of the edges of the nest patch, representing the potential predation risk that is often associated with edges (Andreassen and Ims, 1998), and nest patch proximity index (after Bender et al., 2003), which describes how connected the nest patch is to the rest of the landscape. The composition of each 800-m nest-centred landscape was described using the percent cover of forested habitat. We described landscape configuration using mean patch size and patch density, which together describe how dissected the landscape is. We also used edge density, landscape shape index and mean edge to edge nearest neighbour as representatives of potential predation risk associated with increased edge complexity on its own and relative to patch size and crossing gaps.

A final independent variable was an index of prey density. Because owls mainly eat small mammals (Cannings, 1993), the effects of forest fragmentation on the behaviour and reproductive success of Northern Saw-whet Owls may be modified by fluctuations in prey density (Redpath, 1995a, Hakkarainen et al., 1997). Consequently, we estimated relative prey density in 2003 and 2004 using small mammal trackplates (King and Edgar, 1977; Mabee, 1998). Each trackplate was contained within a 30 cm length of 3.7 cm diameter PVC pipe. The trackplate itself consisted of a plastic board with a two-part chemical dye in the middle and treated paper on either side to record the tracks of any small mammal moving passively through the tube.

Due to logistical constraints, track plating was carried out late during the nestling period during the last two weeks of June in 2003 and 2004. Ten to 30 plates were deployed in within the 800 m radius of the nest along 200 m lines (5 per line). Half of the lines in each landscape were placed along edges and the other half in the forest interior (more than 200 m from the edge). Sampling intensity varied with the amount of forest cover within each landscape with 2 lines (1 interior, 1 edge) in landscapes with forest cover up to 30%, 4 lines (2 interior, 2 edge) in landscapes with forest cover between 31% and 60% and 6 lines (3 interior, 3 edge) in landscapes with greater than 61% forest cover. Trackplates were left out for 10 days (± 2 days) and then removed. Because it was often difficult to identify individual paths, we estimated small mammal density with the number of prints/trackplate/day for each landscape (Whisson et al. 2005).

Statistical Analysis

Statistical analyses were conducted using either SPSS 11.5 (SPSS, 2001) or SAS 9.1.3 (SAS Institute Inc., 2004). Telemetry data revealed that males travelled from perch to perch both within and among patches while foraging. Thus, we examined the relationship between travel distance on time spent at a perch and within a forest patch using a general linear mixed model, including individual male as a categorical random effect. For patch residence time and distance to the next patch, we also included patch size as a surrogate measure for the resources within a patch. Males often moved between perches within a patch before moving to another patch. Thus, we examined the effect of patch size and the distance to the next patch on the number of interperch movements within a patch using a general linear mixed model, again including males as a random effect, with the prediction that males will move between perches more often in larger patches and when the distance to the next patch is large.

We modelled the relationship between each measure of male home range, perch time and condition with the variation in habitat variables within each 800 m radius landscape using Hosmer and Lemeshow's (2000) model building approach modified for general linear models. We began by identifying significant main effects through a univariate linear regression with each independent variable individually. For these tests, we set the two-tailed significance level at $\alpha = 0.25$ to avoid eliminating variables that may become significant when interacting with other variables (Hosmer and Lemeshow, 2000). Once potential main effects were identified, we fit a forced entry model including all possible effects and identified those that remained significant at $\alpha = 0.05$. We then fit a reduced model with only the remaining effects and repeated this process until only significant effects remained. We examined the linearity of effects graphically (James et al., 1990; Bissonetti, 1999) and compared the fit of linear models to either quadratic or natural log relationships when necessary. Lastly, we tested for any biologically reasonable interaction between main effects.

Changes in forest amount are often correlated with changes in forest configuration (Fahrig, 1997). Thus, before beginning the model building process, we examined all habitat variables for correlations between habitat amount (percent cover) and our five configuration variables. When correlation coefficients exceeded 0.60, we accounted for the effect of forest cover by regressing configuration metrics against forest cover using simple linear regression and then using the residuals as corrected independent variables in the model building process (after Villard et al., 1999, Bélisle et al., 2001).

We assessed parental provisioning by modelling the relationship between the number of food loads delivered in a night (nightly provisioning rate) and the habitat variables described above using a general linear mixed model built again using the model-building approach of Hosmer and Lemeshow (2000). Because parental provisioning rates are often affected by the age of the young (Hedd et al., 2002), we included the approximate age of the oldest nestling (days since hatch ± 3 days) as a covariate. We accounted for pseudoreplication within nests by using nest as a random factor. We also examined the relationships between nightly provisioning rate (feeds in a night) and mean perch time for foraging males using a generalized linear mixed model, again including age and nest as additional variables. Lastly, we examined the relationship between mean provisioning rate (feeds/night) and individual reproductive success and juvenile condition introducing clutch size as a covariate when appropriate (after Tremblay et al., 2003).

Results

We obtained foraging behaviour and and enough data points (> 30; Seaman et al., 1999) to estimate home range size from 14 between 2002 and 2005. We calculated telemetry error based on 37 locations of live, tagged owls that were between 26 and 1484 m away from the observers. Telemetry bearing error was unbiased (mean difference between actual and estimated bearings = 0.39°; t = 0.289, P=0.774, df = 77), and the standard deviation of errors was 22.5°. Mean linear error was 62.8 m (± 52.6 SD, n = 38).

Mean perch time and inter-perch distance were calculated for each male from an average of 29 ± 15.5 inter-perch movements per bird (n = 14). The distances males travelled between consecutive perches varied widely from 19 to 1700 m (mean = 320.5 m ± 257.2, n = 398). The time a male spent at each perch ranged from 1 to 60 minutes (mean = 10.9 ± 8.2 min, n = 398). When the variation among males was controlled with a random effect, the time spent at a perch increased significantly with as the distance to the next perch increased ($F_{1,370} = 4.7$, $P = 0.048$; Table 2.1). A significant interaction between perch distance and individual males indicates that the strength of this relationship varied among individuals ($F_{13,370} = 1.9$, $P = 0.026$; Table 2.1).

At the patch level, males foraged for two to 104 minutes in each forest patch (mean = 22.7 min ± 17.8 (SE), n = 69) and the distance between consecutively used patches ranged from 11.2 to 1431.2 m (mean = 131.1 m ± 223.3, n = 69). Patches ranged in size from 0.3 to 438.8 ha (mean = 71.2 ha ± 107.3, n = 69). Once the effect of individual male was accounted for, patch residence time increased most strongly with the size of the patch; but it also increased significantly as the distance to the next patch increased (Table 2.2). Males moved 0 to 10 times between consecutive perches within a given patch (mean = 2.3 ± 2.1, n = 68). The distance to the next patch did not influence the number of movements a male made between perches within that patch

(Table 2.2). As expected, the number of movements increased significantly as patch size increased (Table 2.2).

Movement between perches and foraging behaviour were also related directly to landscape metrics of habitat amount and configuration. The mean time a male spent at a perch while foraging decreased significantly with log-transformed increases in both percent forest cover and nest patch proximity index (Table 2.3). These two variables were not significantly correlated ($r = 0.37$, $P = 0.190$; $n = 14$) and accounted for 75% of the variation in the data ($r^2 = 0.75$, $F_{2,11} = 16.5$, $P < 0.001$). The mean foraging radius of owls decreased significantly as the natural log of edge density increased (Table 2.3) and this relationship explained 36% of the variation in the data ($r^2 = 0.36$, $F_{2,12} = 6.8$, $P = 0.023$)

Analyses of all telemetry fixes for each male provided information on home range size. Home range sizes were estimated from an average of 46.4 telemetry fixes per bird ± 18.4 ($n = 14$) and varied dramatically from 11.7 to 137.0 ha (mean = 89.4 ha ± 40.2, $n = 14$). Contrary to prediction, home range size increased non-linearly with increasing forest cover in nest centred landscapes ($F_{1,10} = 13.2$, $P = 0.005$; Fig. 2.1) and decreased with an increase in edge density ($F_{1,10} = 9.8$, $P = 0.010$; Fig. 2.1) of the landscape and the complexity of the nest patch edge ($F_{1,10} = 10.0$, $P = 0.010$; Fig 2.1). Neither nest patch shape index nor edge density was significantly correlated with percent forest cover ($r = -0.18$, $P = 0.53$ and $r = 0.24$, $P = 0.404$ respectively, $n = 14$). These three factors explained 85% of the variation in male home range size ($r^2 = 0.85$, $F_{3,9} = 16.9$, $P < 0.001$).

Effects of habitat and male behaviour on provisioning rates and reproductive success

Although scales were installed in 43 nests between 2002 and 2004, malfunctions resulted in provisioning data from only 29 nests. At many nests, there were gaps in the data and as a result, nightly provisioning rates (feeds in a night) were calculated over a range of 5 to 25 days per nest (mean = 11.6 days ± 5.0, n = 29). Males delivered between 3 and 10 food loads per night (mean = 7.4 ± 1.2 feeds, n = 336 nights from 29 nests). The number of deliveries in a night decreased as nestlings aged ($\beta = -0.03$; $F_{1,305} = 11.2$; $P = 0.001$).

Larger broods were associated with higher provisioning rates ($F_{1,305} = 27.9$, $P < 0.001$; Fig. 2.2), once the effects of nestling age were accounted for. Provisioning rates also increased significantly with the proportion of forested habitat in the landscape and decreased significantly with increases in the nearest neighbour distance among patches ($F_{1,305} = 5.4$, $P = 0.021$ and $F_{1,305} = 5.6$, $P = 0.019$ respectively; Fig. 2.2).

Males spent less time at a perch, on average, with increasing forest cover and patch proximity (above). Once the variation associated with each of the eight nests for which we could link male perching and provisioning data was accounted for, longer perch times, on average, also led to a decrease in the number of food loads males delivered nightly ($F_{1,82} = 16.3$, $P = 0.001$; Fig. 2.3). There was no significant relationship between male provisioning rates and either their mean foraging radius ($F_{1,81} = 0.1$, $P = 0.471$) or home range size ($F_{1,81} = 0.2$, $P = 0.129$) once the within-nest variation and nestling age was accounted for.

Among the nests for which we could link mean male provisioning behaviour (feeds/night) and nest success through the scale data, clutch size ranged from 3 to 9 eggs (mean = 5.8 eggs ± 1.2, n = 27). These nests fledged from 1 to 6 young (mean = 4.3 fledglings ± 1.4, n = 27). As expected, there was a significant positive relationship between clutch size and the number of young fledged. However, once clutch size was accounted for, there was also a significant positive relationship between the mean number of feeds per night by the male and the number of young that successfully fledged from a nest (Fig. 2.4). Together, these two variables accounted for just over 50% of the variation in the data ($r^2 = 0.51$, $F_{2,24} = 12.4$, $P < 0.001$; Table 2.4).

There was no relationship between the mean ratio of heterophils to lymphocytes (H:L ratio) of juveniles in the nest and provisioning rates ($F_{1,12} < 0.1$, $P = 0.957$). However, the within-nest variation in nestling H:L ratios decreased significantly as provisioning rates increased ($r^2 = 0.29$. $P = 0.044$, $n = 15$; Fig. 2.5), suggesting that there was more variation in the condition of chicks within nests that experienced low provisioning rates.

Effect of habitat and parental effort on male physiological condition

We collected blood samples from 24 males including radio-tagged individuals during the early nestling stage between 2004 and 2005 to obtain heterophil:lymphocyte (H:L) ratios. These ratios varied between 0.48 and 3.13 (mean = 1.29 ± 0.14, n = 24). Higher H:L ratios, which are indicative of chronic stress, increased with brood size and decreased in areas with greater forest cover (Table 2.5). These two variables accounted for 65% of the variation in the data ($r^2 = 0.65$, $F_{2,21} = 19.1$, $P < 0.001$). Male body mass ranged from 70.5 to 87.0 g (mean = 79.8 ± 1.05 g, n = 22), tarsus lengths ranged from 26.6 to 31.1 mm (mean = 28.2 ± 0.26 mm, n = 22). Residual body mass (i.e. after being regressed against tarsus length) increased significantly with both the edge density of the landscape and the residual mean patch size (Table 2.5). These combined effects accounted for 48% of the variance in the data ($F_{2,18} = 8.33$, $P < 0.001$).

Effect of prey availability on male behaviour and condition

As evidenced above, print density, measured through track plating in 2003 and 2004 did not enter into any models explaining male behaviour or physiological condition. A follow-up mixed model analysis of the relationship between print density and the landscape metrics used, while accounting for individual nest variation, revealed that the density of small mammal prints per trackplate per day increased significantly with patch size, once we accounted for the effects of habitat cover in the surrounding landscape ($F_{1,32} = 12.2$, $P = 0.001$; $r^2 = 0.28$).

Discussion

As predicted by the Marginal Value Theorem (Charnov, 1976, Stephens and Krebs, 1986), owls spent more time at a perch as the distance to the next perch increased. However, there was considerable variation both within and among males. For males living in landscapes with large forest patches, most inter-perch movements occurred within patches. Owls nesting in areas with more forest cover and greater connectivity also perched for less time on average, perhaps because they could move more easily within these more contiguous habitats. Similarly, tawny owls (*Strix aluco*), also foraged longer at a perch with increasing interperch distance, with the effect being more pronounced in highly fragmented areas (Redpath 1995a).

The effect of interperch distance on perching time may be most apparent when the next perch is across a gap in the habitat. Indeed, all males in this study spent more time foraging in a patch before leaving as the distance to the next patch increased. Residency time is predicted to increase with patch isolation as a function of decelerating foraging gains that are offset by travel costs (i.e. The Marginal Value Theorem: Charnov, 1976; Stephens and Krebs, 1985). In accordance to this prediction, patch residence time increased significantly with patch size as well as distance to the next patch. Similar relationships have been reported for species as diverse as insects (e.g., Cresswell and Osborne, 2004) and large mammals (e.g. Shipley and Spalinger, 1995). For owls, larger patches may offer more perch options, and possibly a greater abundance of some small mammal prey (Mills 1995; Sunde and Redpath, 2006).

Indeed, small mammal density increased significantly with patch size nest-centred landscapes in this study. Thus, although print density did not directly affect male behaviour and reproductive success as suggested by the models in this study, our measure of patch size may represent a surrogate measure of resource availability. Print density itself may not have been significant due to the incomplete nature of the data.

In addition to the increased foraging opportunities afforded by larger patches, the increase in patch residence time as gap sizes increased likely reflects movement costs. These costs may reflect either an increase in the physiological cost of covering larger distances (Hinsley, 2000) or gap avoidance behaviour as a result of increased predation risk (Bélisle and Desrochers, 2002; Harris and Reid, 2002). Indeed, higher survival associated with remaining in a patch may partially explain why individuals of diverse species remain longer in patches than MVT would predict (Nonacs, 2001). For saw-whet owls, predation risk associated with gaps is likely more important because foraging owls often travelled much longer distances within forest patches than among them and were often observed stopping at a forest edge before leaving a patch. Saw-whets have been recorded as prey for long-eared owls (*Asio otus*) and are likely vulnerable to predation from opportunistic great-horned owls (*Bubo virginianus*) and barred owls (*Strix varia;* Cannings, 1993). All three species occur in the study area (Grossman 2003). Although both great horned and long-eared owls have been associated with landscapes with moderate amounts of forest cover and edge density (Marks et al. 1994; Hinam 2001; Grossman 2003), they are known to hunt from forest edges or in open areas (Glue and Hammond, 1974; Longland and Price, 1991; Rohner and Krebs 1996).

Our results were consistent with our predictions that residence time would increase with the distance between perches and patches. However, they only partially supported our prediction that home range size would vary quadratically with habitat composition and configuration. The home range sizes of male saw-whet owls dropped dramatically in landscapes with low forest cover and large amounts of edge, and home range sizes were much larger in landscapes of moderate forest cover and fragmentation. However, home range size levelled off rather than decreased in the highest ranges of forest cover and decreased with increasing edge density. These results contrast with several other avian studies in which home range sizes were highest in landscapes with low habitat cover and high fragmentation (Redpath, 1995b; Bruun and Smith, 2003; Siffczyk et al., 2003). For some prey species, such as deer mice, landscapes with high forest cover and low edge, may provide poor habitat (Bayne and Hobson, 1998; Silva et al., 2005), forcing males to expand their home ranges in search of more resources (Redpath 1995b; Siffczyk et al. 2003). However, saw-whet owls do not specialize on a single prey species (Cannings 1993) and thus reductions of one prey species with lower forest fragmentation, may be offset by increases in abundance of other small mammal species with greater forest cover (Mills 1995), reducing the effect of prey availability on the spatial arrangement of individuals. Indeed, a study of space use by four different raptor species found no effect of small mammal abundance on where even prey specialists foraged in a landscape, finding instead the need to provision a central place a more important determinant of space use (Thirgood et al. 2003).Individuals breeding in fragmented areas, often exhibit more centralized movements and an increased reluctance to cross gaps (Bayne and Hobson, 2001; Fraser and Stutchbury, 2004). Thus, instead of expanding their home range to offset the effects of patchy resources, individuals may restrict their movements as a result of a greater risk of predation associated with crossing open areas (Turcotte and Desrochers 2003), resulting in smaller home ranges in areas of extreme forest loss fragmentation.

The effects of landscape composition and configuration on male foraging behaviour were also apparent through their effects on provisioning rates and subsequent reproductive success. As predicted, males breeding in more contiguous landscapes with a greater proportion of forest cover provisioned young more frequently than males nesting in more fragmented landscapes. This pattern has been observed in a number of breeding birds (Bruun and Smith, 2003; Luck, 2003; Suorsa et al., 2003; Tremblay et al., 2005; but see Nour et al., 1998). Although provisioning rates were not related to the distance males travelled while foraging (in contrast to Bruun and Smith, 2003; Tremblay et al., 2005), they were closely tied to the mean perch time of foraging males. Again in support of our predictions, males that spent more time, on average, at a hunting perch provisioned the young less often. This increase in perch time may reflect a reduction in foraging efficiency (above), either though a decrease in prey availability (Luck, 2003) or an increase in predation risk in more fragmented areas (Ruiz et al., 2002). In addition to the effects of landscape, male provisioning rates increased with brood size as they do in many bird species (Cucco et al., 1995; Olsen et al., 1998;

Dawson and Bortolotti, 2003; but see Bruun and Smith, 2003). There was no interaction between brood size and landscape characteristics in their effects on provisioning rates, which means that nestlings received more food per capita in more contiguous forest.

Predictably, males that delivered prey less often fledged fewer young, once the effect of clutch size was controlled for. A causal link between delivery rates and fledging success assumes that the number of nest visits is a reliable proxy for the biomass provided to the chicks (Nolan et al., 2001). This assumption seems reasonable in species like saw-whet owls that are limited in the volume of prey that can be carried. Thus, our results are consistent with the studies that link provisioning rates to reproductive success (Ens et al., 1992; Henderson and Hart, 1993; Frey-Roos et al., 1995, Maigret and Murphy ,1997; but see Bruun and Smith, 2003) and support the contention that energy requirements of the young are an important factor limiting the productivity of nesting birds (Martin, 1987; Wiehn and Korpimäki, 1997).

Aside from the number of chicks that fledged, the immunological condition of chicks may provide additional insight into the reproductive success of males because it may be correlated with subsequent chick survival (Christe et al., 1998; Suorsa et al., 2004). Higher levels of chronic stress, as measured through haematological parameters, have been linked with lower juvenile recruitment (Lobato et al., 2005). In this study, there was no relationship between the rate of food deliveries to the nest and mean juvenile heterophil:lymphocyte ratio for all young in a nest. However, males who provisioned the nest less frequently fledged broods with a greater variation in physiological condition among nestlings. Lower provisioning rates may increase food stress for young within the nest leading to a higher incidence of antagonistic behaviour between nestlings (Mock and Parker 1997). These behaviours are associated with spikes in blood corticosterone levels (Kitaykski et al., 2001), and repeated spikes may result in chronic stress, manifested by higher heterophil-lymphocyte ratios (Gross and Siegel, 1983).

In species like saw-whet owls, which hatch their eggs asynchronously (Cannings, 1993), stress is often correlated with hierarchies in the nest, with higher levels in smaller, younger nestlings (Schwabl, 1999; Tarlow et al., 2001; Love et al., 2003). This disparity is generally exacerbated by food shortage (Kitayski et al., 1999). Because chronic stress in the form of immunosuppression may lower survival (Christe et al. 1998; Suorsa et al. 2004), this may be a mechanism to effect adaptive brood reduction when available resources cannot support the entire brood (*sensu* Lack, 1947, Mock and Parker, 1997).

Variation in landscape characteristics also affected the condition of males directly, as reflected by body size and H:L ratios. As predicted, chronic physiological stress measured through H:L ratios was higher in males breeding in landscapes with lower amounts of forest cover. In these habitats, stress may result from an increased rate of encounters among conspecifics or with predators (Ruiz et al., 2002; Perez-Tris et al., 2004) or from a perception that the landscape is more dangerous, both of which could result in more frequent spikes in blood corticosterone (Clinchy et al., 2002), ultimately leading to higher H:L ratios through a reduction of lymphocytes in the peripheral blood (Hõrak et al., 1998). Because lymphocytes are responsible for an individual's immune response, low lymphocyte numbers may reduce immunocompetence and expose individuals to an increase in infection and parasitism (Gross and Siegel, 1983; Hõrak et al., 1998; Ruiz et al., 2002). Even birds exposed experimentally to predators exhibited reduced immunocompetence and increased parasitism (Navarro et al., 2004).

The effect of landscape composition on male physiological condition in this study was exacerbated by brood size. Males feeding larger broods had significantly higher heterophil:lymphocyte ratios suggesting that higher brood demands generate chronic stress. This effect of increased brood size on parental costs of reproduction is ubiquitous in birds (Hegner and Wingfield, 1987; Hõrak et al., 1998; Ardia, 2005) and mammals (Huber et al., 1999; Oksanen et al., 2002; Koivula et al., 2003). Whether from landscape or brood characteristics, higher levels of chronic stress are likely to reduce the health of males with cascading fitness implications. Other field studies of birds have shown that a reduction in immunocompetence as a result of higher levels of chronic stress can reduce subsequent survival (e.g., Saino et al., 1997) and reproductive success (Hanssen et al., 2003; Hanssen et al., 2005). Unfortunately, male site fidelity in northern saw-whet owls is low both in this study and in other areas (Cannings, 1993; Marks and Doremus, 2000) and so it was impossible to determine the relationship between immunocompetence in one season and fitness in the subsequent year.

Contrary to expectations, males were heavier relative to body size in landscapes with greater amounts of habitat edge and larger patch sizes. Body mass may be a function of at least two competing influences (Ots et al., 1998). An increase in prey availability in landscapes with larger patches and increased habitat edge (Mills 1995; Bayne and Hobson 1998; Tallmon et al., 2003) may result in higher body masses, while an increase in predation risk often associated with increased edge habitat (Andreassen and Ims, 1998) may result in birds losing mass in an effort to increase mobility (Hedenström, 1992; Witter and Cuthill, 1993). However, predation risk may also work in the other direction, especially in species such as saw-whet owls, which employ an anti-predator strategy that involves concealment (Sealy and Hobson, 1987) rather than flight. Regular encounters with predators often interrupt feeding (Pravosudov and Grubb, 1998) and thus individuals may maintain higher body masses relative to size to negate the detrimental effects of lost feeding time (Houston and McNamara, 1993; McNamara et al., 2005).

Conclusions

Habitat loss and fragmentation affected the behaviour of a species occupying multiple habitat patches, with associated effects on reproductive success. Such relationships have been shown only occasionally (e.g. Frey-Roos et al., 1998; Luck, 2003) despite the hundreds of studies that have been published on the effects of habitat fragmentation. Saw-whet owls nesting in landscapes with low forest cover and high fragmentation maintained smaller home ranges and spent more time perching during foraging activities, which led to lower provisioning rates. Lower provisioning rates were associated with males that fledged fewer young and young with a greater variation in condition within broods. Finally, males breeding in landscapes with low forest cover and high fragmentation exhibited high levels of immunological stress and males inhabiting landscapes with high edge density and larger mean patch size were heavier overall. Thus, it appears that landscape characteristics generated differences in foraging behaviour and foraging behaviour produced differences in reproductive success.

Despite the strong suggestion of causal links between the successive effects of forest fragmentation (encompassing composition and configuration), provisioning rates and reproductive success, more specific information is still needed. In particular, future investigations of the mechanics underlying the effect of habitat variation on individual fitness would benefit from a more thorough understanding of species habitat preferences. This would increase the resolution of the study by ensuring that habitat and non-habitat is as accurately defined as possible. Studies of this nature would also be best focussed on populations containing individuals that could be followed over a number of years. Tracking juvenile survival and future reproductive investment would be an important step in fleshing out our understanding of the relationship between habitat changes and individual fitness and, ultimately, population viability.

Table 2.1..Coefficients and significance of a mixed-effects generalized linear model describing the relationship between the distance to the next perch and the time (min) that a male spent at each perch, using individual males (each from a different nest site, n = 14) as a categorical random effect.

Parameter	β	df	*F*	*P*
Distance to next perch	0.01	1	4.74	0.048
Individual male		13	1.42	0.148
Distance X individual male		13	1.93	0.026
Error		370		

Table 2.2. Summary of results of two general linear mixed models of the effects of patch size and distance to the next patch on individual patch residence time of foraging males (n = 14) and the number of sequential perches a male visits within a patch.

Dependent variable	Parameter	β	df	F	P
Patch residence time	Patch size	0.07	1	20.1	<0.001
	Distance to next patch	0.02	1	4.2	0.045
	Individual male		11	0.7	0.754
	Error		55		
Number of sequential perches in a patch	Patch size	0.01	1	38.3	<0.001
	Distance to next patch	0.00	1	0.2	0.684
	Individual male		11	1.6	0.140
	Error		54		

Table 2.3. Summary of results of general linear models of mean perch time and mean foraging radius of 14 radio-tagged male northern saw-whet owls and significant effects of habitat amount and configuration. Each model includes parameter estimates for all variables that significantly improved the fit of the model.

Dependent Variable	Parameter	β	SE	t	P
Mean perch time	ln(percent cover)	-6.83	1.55	-4.41	0.001
	ln(proximity index)	-1.44	0.66	-2.19	0.051
	Intercept	48.07	6.18	7.78	<0.001
Mean foraging radius	ln(edge density)	-743.7	285.74	-2.6	0.023
	Intercept	3851.06	1200.4	3.21	0.008

Table 2.4. The results of a general linear model testing the provisioning rate on the number of young fledged from 27 nests including clutch size as a main effect.

Parameter	β	SE	t	P
Provisioning rate	0.96	0.23	4.11	< 0.001
Clutch size	0.52	0.16	3.16	0.004
Intercept	-5.87	2.07	-2.84	0.009

Table 2.5. Results of a general linear model of the effects of landscape variation and brood size on immunological condition (heterophils:lymphocytes) and body condition (mass:tarsus length) of breeding male owls.

Dependent Variable	Parameter	β	SE	t	P
Heterophils:Lymphocytes	Percent cover	-0.02	0.01	-4.89	<0.001
	Brood size	0.17	0.07	2.38	0.027
	Intercept	1.61	0.46	3.52	0.002
Mass:tarsus	Edge density	0.17	0.06	3.01	0.008
	Mean patch size residual	0.07	0.02	3.61	0.002
	Intercept	-10.75	3.7	-2.90	0.010

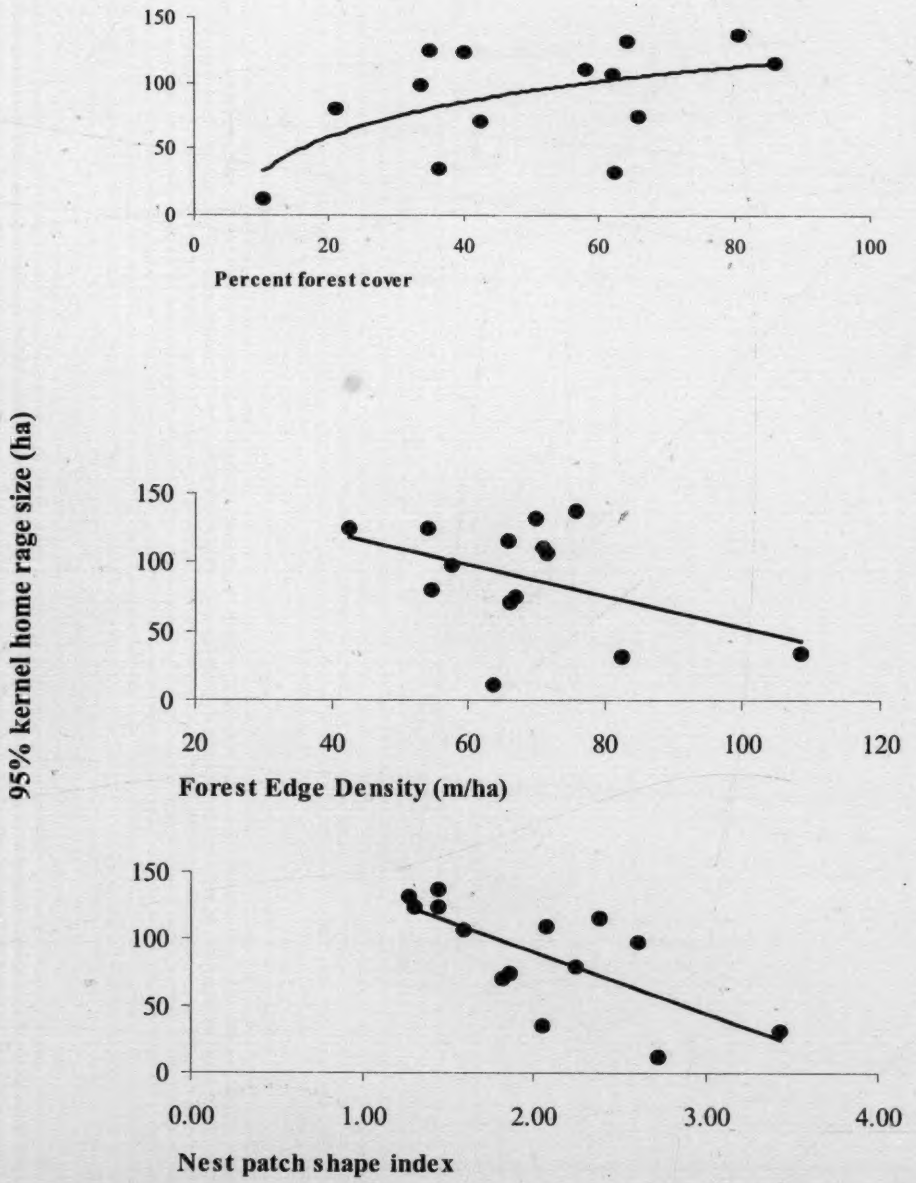

Figure 2.1. The relationship between male saw-whet home range size (95% fixed kernel estimator) and each of percent forest cover, forest edge density and nest patch shape index. Male home range size (n = 14) increased logarithmically with increasing forest cover and decreased in landscapes with greater amounts of edge and in nest patches with more complex edges (higher nest patch shape index).

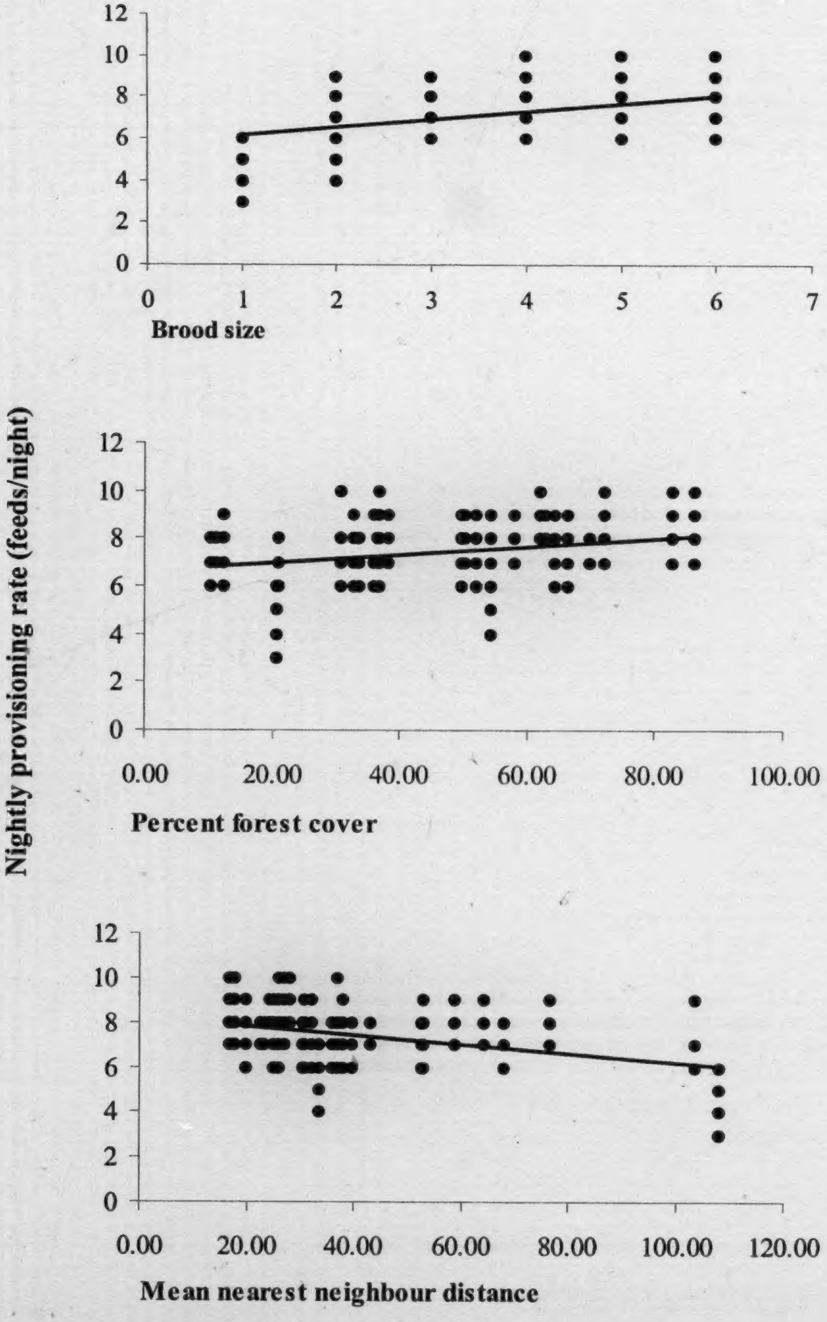

Figure 2.2. The relationship between nightly provisioning rate (number of feeds in a night) for 29 males and changes in brood size, percent forest cover and mean edge-to-edge nearest neighbour distance (metres).

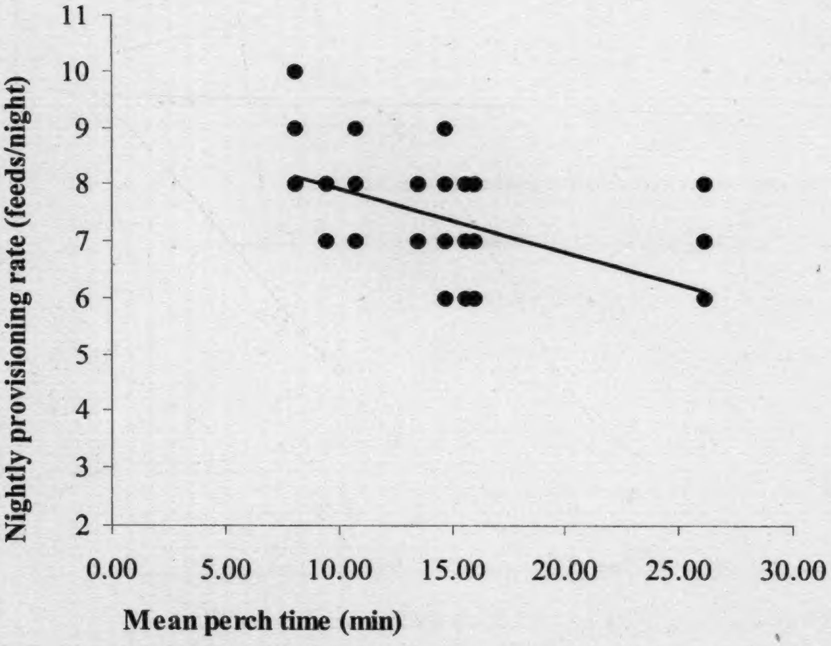

Figure 2.3. The relationship between the nightly provisioning rate (number of feeds in a night) and the mean time spent at a perch (min) by each foraging male for which there was corresponding scale data (n = 8).

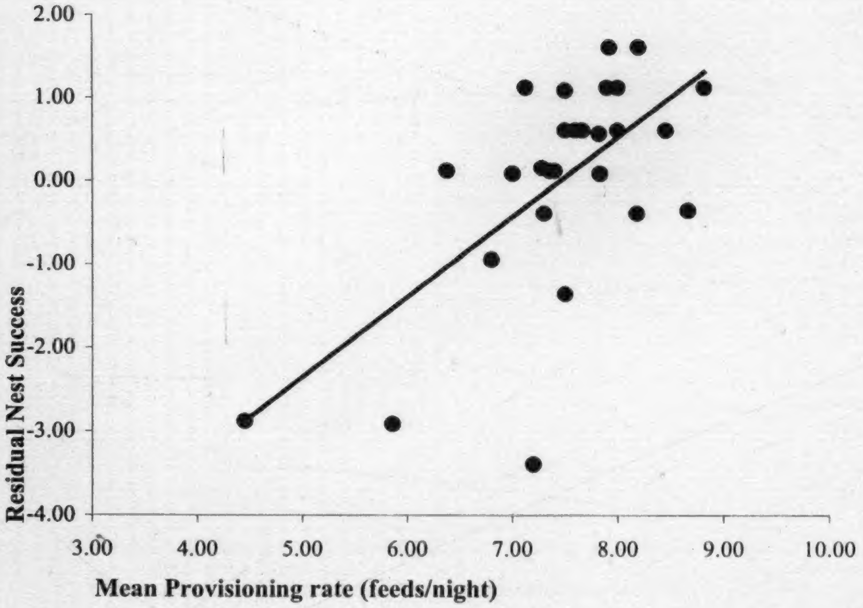

Figure 2.4. The relationship between nest success (number of fledglings produced after accounting for clutch size) and the mean rate at which males provision the nest (number of feeds/night) for the 26 males for which corresponding nest success and scale data existed.

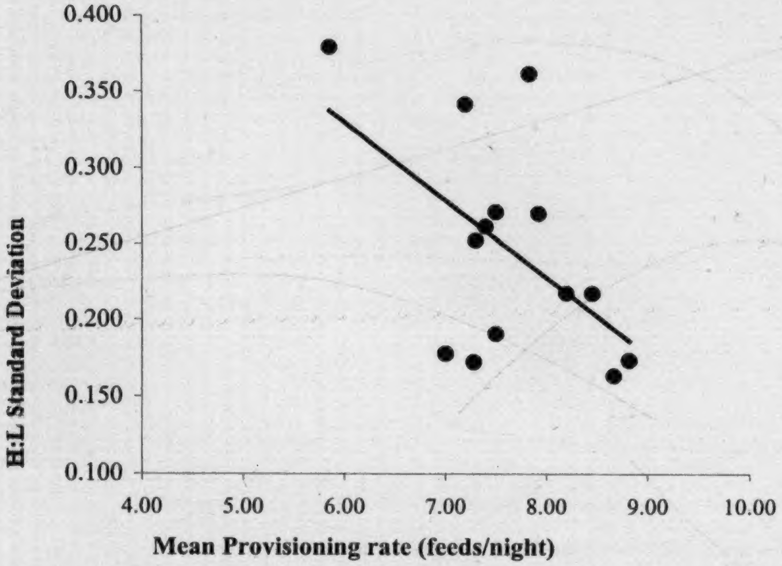

Figure 2.5. The relationship between the number food deliveries per night (mean provisioning rate) to the nest by each of 15 males and the standard deviation of the ratio of heterophils to lymphocytes (H:L standard deviation) in peripheral blood of all the chicks in a nest.

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Chapter 3 - Habitat loss and fragmentation limit the reproductive success of Northern Saw-whet Owls through reduced brood size and juvenile condition

Introduction

Habitat loss and fragmentation are some of the most pervasive threats to bird populations (Rolstad 1991). A reduction in the amount of habitat, decreases in remaining fragment size and an increase in habitat edge have been associated with lower reproductive success in numerous species of birds (e.g. Hoover, Brittingham & Goodrich. 1995; Robinson *et al.* 1995; DeSanto *et al.* 2002). However, the majority of work on the effects of habitat composition and configuration on avian reproduction has focussed on open-cup nesting passerines. This work has identified nest predation and brood parasitism as the main causes of lower nest success in breeding birds (see Stevens *et al.* 2003 for review). The response of cavity nesters to habitat loss and fragmentation is less clear. While some studies have found no relationship between habitat composition and configuration and nest success (Matthysen & Adriaensen 1998; Huhta & Jokimäki 2001), others have found lower reproductive success in landscapes with less forest cover (Mazgajsk & Reijt 2006) and greater amounts of habitat edge (Deng & Gao 2005). Although nest predation rates are usually much lower in cavity nesting species (Møller 1991; Loman 2003; Lampila, Mönkkönen & Desrochers 2005; Deng & Gao 2005; Mazgajsk & Reijt 2006), several studies have found lower reproductive success in cavity nesters occupying more fragmented habitat relative to more contiguous landscapes (Loman 2003; Mazgajsk & Reijt 2006; Lampila *et al.* 2005). This suggests that mechanisms other than nest predation may be driving the effects of habitat loss and fragmentation on these species, but no general cause has been identified.

Lower reproductive success in areas with less forest cover and smaller fragments may result from (1) smaller clutch sizes (Mazgajsk & Reijt 2006), (2) lower nestling survival rates, or (3) poorer nestling condition (Møller 1991; Hinsley, Rothery & Bellamy 1999; Hakkarainen *et al.* 2003; Loman 2003; Mazgajsk & Reijt 2006). The latter two effects presumably result from the effects of changes in habitat composition and configuration on the foraging conditions experienced by provisioning parents (Mazgajsk & Reijt 2006) or through lower food availability, especially in predatory species (Körpimaki & Norrdahl 1991, Körpimaki 1994; Brommer, Pietianen & Kolunen 2002). Indeed, lower provisioning rates generally appear to cause slower nestling growth (Richer 1989; Henderson & Hart 1993; Shawkey, Bowman & Woolfenden 2004), greater variation in nestling condition (Kitayski *et al.* 1999; Hinam & St Clair unpublished data), and reduced reproductive success (Maigret & Murphy 1997, Hinsley *et al.* 1999, Hinam & St Clair unpublished data).

For many cavity nesting species with low rates of nest predation, the link between variation in nestling condition and lower reproductive success may be caused by brood reduction (Shawkey *et al.* 2004). Brood reduction occurs when the smallest members of the brood perish before fledging and may provide a mechanism by which parents can adjust the number of young in a nest to the available resources and thus fledge the highest possible number of healthy offspring (Lack 1947; Stoleson & Beissinger 1995;

Mock & Forbes 1997; Valkama, Korpimäki & Holm 2002). Limited food resources and reduced parental provisioning rates have been associated with brood reduction (Magrath 1989; Shawkey *et al.* 2004). Typically, these broods are also characterized by hatching asynchrony, which provides a competitive advantage to earlier-hatched young (Love, Bird & Schutt 2003; Shawkey *et al.* 2004).

In the absence of overt aggression among siblings (e.g., Shawkey *et al.* 2004), limited food may simply lead to a greater disparity in condition between early and late hatched nestlings (Schwabl 1999; Tarlow, Wikelski & Anderson 2001; Love *et al.* 2003) to facilitate brood reduction (Shawkey *et al.* 2004). For nestlings in these broods, higher levels of chronic stress may result both from food shortage (Shawkey *et al.* 2004) and increased competition among nestlings (Kitayski *et al.* 1999). Because changes in habitat composition and configuration can cause a reduction in resources (Siffczyk *et al.* 2003; Sunde & Redpath 2006), or change the accessibility of resources and the efficiency with which parents can exploit them (Hinsley 2000; Hinam & St. Clair unpublished data), it is logical to assume it can also reduce provisioning rates and promote brood reduction. In Florida scrub-jays (*Aphelocoma coerulescens*), higher rates of brood reduction have been recorded in suburban populations (Shawkey *et al.* 2005), compared to rural, however, there have been no studies to our knowledge linking the incidence of brood reduction to habitat fragmentation

One reason that the effects of habitat loss and fragmentation on reproductive success in cavity nesters have been equivocal may be the scale at which fragmentation effects on birds have usually been assessed. Most studies have focussed on individuals occupying a single patch (e.g. Matthysen & Adriaensen 1998; Loman 2003; DeSanto *et al.* 2002; see Stevens *et al* 2003 for review). However, changes in habitat amount and configuration may have more profound effects on species where individual home ranges encompasses multiple habitat patches, often separated by an inhospitable matrix (Hinsley 2000; Stevens *et al.* 2003). For species that move regularly between patches within their home range, the increasing isolation of those patches may lead to lower provisioning rates to the young (Hinsley 2000; Hinam & St. Clair unpublished data), resulting in slower growth rates, poorer nestling condition and a greater disparity in condition between young; conditions that could be expected to lead to brood reduction and lower reproductive success.

The northern saw-whet owl (*Aegolius acadicus*) provides an opportunity to better understand how changes in habitat composition and configuration affect individual reproductive success. Saw-whets are small, forest-dependent cavity nesters (Cannings 1993). Where they breed at the edge of their range in Alberta, Canada, individuals occupy home ranges that usually encompass multiple habitat patches of forest interspersed in a mainly agricultural matrix. The objective of this study was to examine how variation in forest amount and configuration affected growth rate, and physiological condition of nestling northern saw-whet owls. We also examined how landscape-level habitat loss and fragmentation affected nestling physiology and how both related to fledging success and the occurrence of brood reduction. We predicted that lower forest cover and increased forest fragmentation surrounding nesting locations would result in: (1) slower nestling growth rates, (2) higher measures of physiological stress, (3) greater disparity in condition among young within nests, (4) higher rates of brood reduction, and (5) lower nest success relative to initial brood size.

Methods

Study area and species

Our study area was comprised of woodlots in the transition zone between the boreal forest and aspen parkland within a 3,040 sq-km area of east-central Alberta, Canada (53° 32' N, 113° 33' W; Fig. 3.1). It was characterized by a patchy distribution of mature mixedwood forest, fragmented primarily by agricultural clearing. As part of a long-term monitoring program for saw-whet owls that began in 1985, approximately 250 nest boxes were erected on private lands. Landscapes within 800 m of active nests contained 10 to 85 percent forest cover and mean edge-to-edge nearest neighbour distances between patches ranged from 15.3 to 122.2 metres (Table 3.1). The owls feed primarily on red-backed voles (*Clethrinomys gapperi*) and deer mice (*Peromyscus maniculatus*) in this study area and elsewhere in Canada (Cannings 1993; Hinam and St.Clair unpublished data).

Nestling Growth rates

Nest box checks began in early April between 2002 and 2005, inclusive. Because saw-whet owls are prone to nest abandonment when disturbed during the early egg-laying period (Cannings 1993), it was not possible to determine the initiation date for most nests. However, once they were discovered, nests were inspected periodically to monitor hatching (when possible). We monitored nestling growth rates using an automated weighing system installed in nest boxes. This system included a weighing platform, which was inserted into the box under the nest contents, and a data recorder, which was connected via a wire and placed at the foot of the tree. To reduce the risk of desertion, we installed the scales as soon after hatching as possible, usually before all the eggs had hatched. The weighing platform measured the mass of the nest box contents (young, nesting material and female) at one-minute intervals, 24 hours a day, and these data were recorded on removable memory modules. Each scale was calibrated at the beginning and end of each nesting season using a 300 g weight. As nestlings aged, regurgitated pellets and debris accumulated on the bottom of the nest, forming a pellet pad. We assumed that this pad grew at a similar rate to the young. However, after approximately two weeks, this pellet pad was quite large and often clung to the side of the box, possibly reducing the ability of the scale to accurately detect changes in mass. Consequently, we calculated growth rate for only up to the first two weeks, when growth of nestlings is essentially linear (Cannings 1987). Linear growth curves have also been recorded in the early stages of nestling development in a number of species (e.g. Platteeuw et al. 1995; Kortner & Geiser 1999; Ramos et al. 2001; Hegyi et al. 2006). Scales were sensitive to ambient temperature resulting in an underlying cyclical pattern of an increase in mass as temperature increased during the day and a decrease in mass of the nest contents as temperature decreased at night (Fig. 3.2). Still, the long-term trend was for an increase in mass as nestlings aged. Growth rate was calculated for the entire nest contents using the slope of a linear regression of the mass recorded at each minute and described as an increase of grams/day (Fig 3.2).

Nestling condition

Nests were checked near the time of fledging (20 to 30 days after discovery, depending on the age of young when discovered) and all remaining juveniles in the nest were assessed for physiological condition. Because young saw whets are hatched asynchronously (Cannings 1993) juveniles vary in size, and so body condition was assessed as the residual of body mass regressed against the length of the left tarsus (Ots, Murumägi & Hõrak 1998). For each nest, we examined the effects of habitat composition and configuration on both means and coefficients of variation for nestling residual mass.

We measured juvenile immunological condition at the time of fledging using the ratio of heterophils to lymphocytes (H:L ratio). In general, higher H:L ratios in the blood are indicative of repeated spikes in corticosterone levels which are assumed to result from chronic stress (Gross and Siegel 1983; Ruiz *et al.* 2002). We collected less than one cc of blood into a heparinized capillary tube by puncturing the ailar vein using a 27 ½ gauge needle. We then prepared one or two whole blood smears per bird using a 2-slide wedge method (Campbell 1988). Slides were stained no later than four months after collection using a Wright stain and a buffer containing de-ionized water and a 2% Giemsa stain solution (Sigma). We used the clearest of the two smears to perform a leukocyte differential, classifying a random sample of 100 white blood cells on a slide into each of five cell types: heterophils, lymphocytes, monocytes, eosinophils and basophils (Campbell 1988). We calculated the H:L ratio by dividing the number of heterophils to lymphocytes from that differential (Gross & Siegel 1983; Campbell 1988). We used the mean and coefficients of variation of H:L ratios within nests as dependent variables to characterize the effects of habitat composition and configuration.

Brood Reduction and Reproductive Success

We recorded the clutch size once laying was completed, brood size after all viable eggs had hatched and the number of young fledged for each nest. Because the occurrence of complete nest failures was low (6.4 %), we measured reproductive success as the number of young fledged in each nest. Brood reduction was inferred when the last-hatched nestling(s) disappeared from nests or were found dead at the bottom of a nest that subsequently fledged some young (after Shawkey *et al*. 2004).

Forest composition, Configuration and food availability

We examined the effect of one measure of landscape-level forest composition, three nest patch metrics and four landscape-lever forest configuration metrics on the growth rate, nestling condition, brood reduction and reproductive success of saw-whet owls. We calculated these metrics using a binary GIS layer of forest and non-forest created by merging 4-m^2 resolution 1998 Indian Remote Sensing data with LANDSAT data from the same year. Landscapes were defined as 800-m radius circles centred on each active nest. This radius was based on the mean foraging distance of male saw-whet owls tracked during the breeding season (Hinam & St. Clair unpublished data), and is thus the area around the nest that is most likely to influence the nestlings via parental provisioning. We measured habitat composition as the percent forest cover within each nest centred 800-m circle. Nest patch size, shape index and proximity index (Bender *et al.* 2003) were used to examine the patch-level effects. We used the landscape-level metrics of edge density and landscape shape index (McGarigal & Marks 1995) to describe the complexity of each landscape. We used mean patch size and patch density to describe the number and size of foraging patches and mean edge-to-edge nearest neighbour distance to describe the accessibility of these patches.

We attempted to account for any possible confounding effects of food availability on the effects of habitat variability by including a measure of prey density for each 800-m radius, nest-centred landscapes in 2003 and 2004 using small mammal track plates (King & Edgar 1977; Mabee 1998). Trackplates consisted of a 28-cm long plastic board, on which was mounted an inkpad, surrounded by strips of treated paper on either side. The board was contained within a 30-cm length of 3·7 cm diameter PVC pipe. A two-part chemical dye recorded the footprints of small mammals moving passively through the tube. Trackplates were placed along 200-m transects, with a board at each 50-m interval. We deployed 2 to 6 transects within each 800-m nest-centred landscape, depending on the amount of forest cover, during the 2003 and 2004 breeding seasons. One half of the transects in each landscape were placed along forest edges and the other half were placed in the forest interior (> 200-m from the edge). Track plates were deployed later in the nestling season (mean fledging date of first young = 19 June ± 18 days (SD), in late June. We left the trackplates in place for 10 days (± 2 days) and then removed them. Prey density was estimated as the total number of prints per track plate per day in each landscape (Whisson et al. 2005)

Statistical Analyses

Statistical analyses were conducted using either SPSS 11.5 (SPSS 2001) or SAS 9.1.3 (SAS Institute Inc. 2004). We modelled the effects of variation in habitat composition and configuration on nestling growth rates, juvenile fledging condition and clutch size using general linear models and a modified Hosmer and Lemeshow (2000) model building approach. Because the clutch size for Northern Saw-whet Owls in this study area varied widely (3-9 eggs), we described reproductive success, which encompassed all sources of nestling mortality, as the number of young fledged and included clutch size as a covariate in the model building process (after Tremblay *et al.* 2003). Consequently, we modelled the relationship between reproductive success and the variation in landscape characteristics using a general linear mixed model. Because changes in habitat configuration may often vary in conjunction with changes in habitat composition (Fahrig 1997), we examined all nest patch and landscape configuration metrics for a linear correlation with habitat composition before beginning the model-building process. In cases where correlation were statistically significant ($P < 0.05$), we accounted for the effect of forest cover by regressing configuration metrics against forest cover using simple linear regression and then using the residuals as corrected independent variables in the resulting model (*sensu* Villard, Trzcinski, & Merriam 1999, Bélisle Desrochers & Fortin 2001).

We constructed our models by first identifying main effects through a series of univariate linear regressions. For these regressions, we used an α of 0.25 in order to avoid missing variables that may have a significant effect on the reproductive success when interacting with other variables (Hosmer & Lemeshow 2000). Once we had identified all possible main effects, we fit a saturated forced entry mixed effects model. Year was also included as a categorical random effect to account for possible interannual variation in breeding conditions. At each step we removed the least significant effect (based on a an $\alpha = 0.05$) until only significant effects remained. We assessed the linearity of remaining main effects by comparing their fit to quadratic terms and added, one at a time, all biologically-relevant two-way interactions.

We modelled the effects of landscape variation and nestling physiological condition on the occurrence of brood reduction within nests using multiple logistic regression and the same model building approach (Hosmer & Lemeshow 2000). We considered both landscape metrics and M:T and H:L means and coefficients of variation as candidate factors in one model. We used the Hosmer and Lemeshow (2000) statistic to assess model fit and the maximum rescaled R^2, which rescales the general R^2 of logistic regression to a scale of 0 to 1 as found in linear regression, to describe the predictive power of the final model (Nagelkerke 1991; Allison 1999).

Results

Nestling Growth Rates

Nestling growth data were obtained from 17 nests. We calculated the rate of growth of the entire nest contents over the first 8 to 13 days (mean = 11.1 ± 1.7 days) of development for 17 nests between 2002 and 2004. Nest contents increased in mass at an average rate of 26.6 ± 11.84 g/day. Linear slopes accounted for 52 to 95% of the variation in the raw data (mean $r^2 = 0.761 \pm 0.117$ (SD)). Larger broods did not exhibit faster growth ($F_{1,15} < 0.01$, $P = 0.979$). Nestling growth was however, affected by forest configuration but not composition or prey density. Nest growth rate decreased significantly as the mean nearest neighbour distance between landscape patches increased (Fig. 3.3; $F_{1,15} = 12.08$, $P = 0.003$) and this relationship accounted for 45% of the variation in the data. The relationship was qualitatively similar when the outlier was removed ($F_{1,14} = 4.39$, $P = 0.055$, $r^2 = 0.24$)

Nestling condition

We measured residual body mass of nestlings just prior to fledging in 34 nests between 2004 and 2005. Neither the mean residual body mass for each nest or the within-nest variation in residual body mass was significantly explained by any of the landscape and prey metrics used in this study (mean residual body mass: $F_{1,32} < 1.41$, $P > 0.244$ for all landscape variables; $F_{1,12} = 0.02$, $P = 0.89$ for print density; residual body mass variation $F_{1,32} > 2.97$; $P = 0.095$ for all landscape variables; $F_{1,12} = 2.58$; 0.134 for print density).

Blood samples were taken from all the young within each nest where the young survived to fledging during the 2003 to 2005 breeding seasons (n = 45 nests). The mean ratio of heterophils to lymphocytes did not vary significantly with any metric of habitat composition or configuration. However, the within-nest variability in H:L ratios (H:L coefficient of variation) decreased significantly as the mean patch size within a landscape increased (Table 3.2; $F_{1,43} = 4.25$, $P = 0.005$, $r^2 = 0.09$), although this relationship accounted for only about 10 % of the variation in the H:L ratios. Neither measure of nestling physiological condition was affected by brood size or print density.

Brood Reduction

We were able to determine whether or not brood reduction occurred in 52 nests between 2002 and 2005. However, twelve nests were not considered because we had not collected physiological data for these nestlings. Of the 40 nests we used, brood reduction occurred in 17. As predicted, nests in which brood reduction occurred had larger broods (Fig. 3.4; *Wald* = 4.22, $P = 0.040$) and higher H:L coefficients of variation (Fig. 3.4; *Wald* = 5.35, $P = 0.021$). Variation in composition, but not configuration, of the surrounding landscape also affected the occurrence of brood reduction. As expected, nests that exhibited brood reduction occurred in landscapes with lower amounts of forest cover (Fig 3.4; *Wald* = 4.82, $P = 0.028$). Together, these variables accounted for 54% of the variation in the occurrence of brood reduction (overall χ^2 = 10.26 df = 3, P = 0.017) and produced a model with a good fit to the data (Hosmer & Lemeshow goodness of fit statistic = 7.37, df = 8, P = 0.497).

Reproductive Success

Females produced clutches of 3 to 9 eggs (mean = 5.6 eggs ± 0.99; n = 75) and hatched broods ranging in size from 1 to 6 nestlings (mean = 4.4 ± 1.25 young; n = 75). The variation in clutch size was not significantly explained by any of the landscape or prey metrics used in this study ($F_{1,73} < 2.43$, $P > 0.124$ for all landscape variables; $F_{1,28} = 0.37$, $P = 0.548$ for print density). The incidence of complete nest failure was low (6.4 % n = 78) and nests fledged 0 to 6 juveniles (mean = 3.7 ± 1.55; n = 73). Nests located in landscapes with greater forest cover fledged significantly more young once the positive relationship between number of fledglings and clutch size was accounted for as a random covariate (Fig. 3.5; general linear mixed model $F_{1,60} = 6.78$, P = 0012).

Discussion

Low forest cover and increased fragmentation reduced individual fitness in northern saw-whet owls though effects on nestling growth rate, physiological condition and ultimately nestling survival. We found a strong negative relationship between the growth of all the chicks within a nest and the mean distance to the nearest neighbouring patch within each nest-centred 800-m landscape. This suggests that owl chicks grow less rapidly when their parents must travel farther distances in their multi-patch territories. The need to travel farther to reach scattered resources has resulted in lower nestling growth rates in other species (Bradbury *et al.* 2003) and lower nestling growth rates have been recorded in more fragmented habitats (Bradbury *et al.* 2003; Granbom & Smith 2006; but see DeSanto *et al.* 2002). However, despite the apparent link between parental provisioning and nestling growth rates (Tobon & Osorno 2006), the relationship found between habitat variation and growth is often weak (Bradbury *et al.* 2003), species-specific and less important than immediate food abundance (Granbom & Smith 2006), unlike the relationship described in this study.

Although nestlings grew at a slower rate in more fragmented landscapes, mean nestling body condition, both in terms of residual body mass and heterophil:lymphocyte ratios, did not vary with habitat composition or configuration. The within nest variation in nestling body mass, corrected for age, also did not vary with changes in habitat. These results were surprising because others have found that birds breeding in smaller patches produce nestlings in overall poorer condition (Lens & Dhondt 1994; Suorsa *et al.* 2004). In addition, although there has been little study on the effects of habitat on the variation in nestling condition, birds nestling in apparently low quality habitats have been found to raise broods with greater variation in body condition (Shawkey et al. 2004). In our context, we might have expected owls nesting in landscapes with less forest and greater patch isolation to generate lower growth rates (above) and nestlings in poorer body condition with a greater disparity among nestlings in the asynchronous broods that characterize saw-whet owls.

Although there were no habitat-induced differences in mean nestling condition, we did find an increase in the variability in immune condition among nestlings within broods. Owls breeding in landscapes with smaller patches raised broods with a greater within nest variation in nestling chronic stress. This increase in variability in nestling condition within a nest may have ramifications on brood reduction and ultimately reproductive success.

The larger coefficients of variation in H:L ratios in broods that were raised in landscapes with smaller mean patch sizes suggests that habitat change affects provisioning rates, potentially by forcing parents to forage through more scattered resources (Bruun & Smith 2003) or through lower prey availability (Mills 1995; Hinam and St Clair in review). However, the effects of lower provisioning rates may only be experienced by some members of the brood. In species with overt sibling aggression, increased food stress often leads to an increase antagonistic behaviour (reviewed Mock & Parker 1997; see also Gonzáles *et al*. 2006). Greater incidents of sibling antagonism has been linked to an increase in the frequency of spikes in the levels of blood corticosterone (Kitayski *et al*. 2001), depressing the immune system (Besedovsky & del Rey 1996) and potentially leading ultimately to higher nestling H:L ratios (Gross & Siegel 1989; Ilmonen et al. 2003). Even without overt aggression, chick stress can be correlated to nestling hierarchy within a brood (Schwabl 1999; Love *et al*. 2003). Thus, in asynchronously hatched species, such as saw-whet owls, food stress as a result of habitat fragmentation, as evidenced by lower provisioning rates in landscapes with less forest cover and greater patch isolation (Hinam and St Clair unpublished data) is likely to increase the disparity in nestling condition.

In addition to the variation we measured in the body and blood condition of chicks, we might have expected food-stressed chicks to exhibit slower growth rates (Nilsson & Svensson 1996; Lago, Johnson & Albrecht 2000; Brzek & Konarzewski 2001). We would also expect this effect to be most apparent for the youngest, least competitive, nestlings (e.g., Nilsson & Svensson 1996). Different growth rates may also result from sexual size dimorphism (Krebs 1999) or brood size (Donald *et al.* 2001). Unfortunately, our method of measuring growth, based on automatic scales in the bottom of nests, does not permit an examination of within nest variation which might further illuminate the patterns of variation in body size and blood components.

Despite the limitation of our growth data, the heightened variation we found in chick stress levels provides important information for interpreting the patterns of brood reduction we observed. We found that brood reduction was more likely to occur in nests with large broods and in areas of low forest cover. It was also more likely to occur when the disparity in nestling H:L ratios was high, presumably as an expression of adaptive asymmetries in competitive ability (*sensu* Lack 1947, Mock & Parker 1997). Many studies have found a link between an increase in the occurrence of brood reduction and larger broods (Valkama *et al.* 2002; Kalmback & Becker 2005; Torres & Mangeaud 2006), most likely because parents of large broods have more difficulty meeting the demands of all nestlings (Valkama *et al.* 2002). Because there was no interaction between the effect of forest cover and initial brood size, it appears that parents do not adjust clutch size to forest composition. The second relationship, that brood reduction was associated with increased variability in H:L ratios is supportive of the adaptive function of hatching asynchrony (above). But it is also possible that inherently higher variation in H:L ratios creates the circumstances that result in brood reduction. Unfortunately, the timing and frequency of our nest visits do not allow us to relate the variation in H:L ratios directly to the degree of hatching asynchrony exhibited by broods. Whatever the direction of this causal relationship, the fact that lower immunocompetence lessens juvenile survival in other species (e.g., Christe, Møller & deLope 1998; Suorsa *et al.* 2004) suggests that high variation in H:L ratios may be associated with brood reduction.

Although brood reduction has been understood for 60 years as a mechanism by which parents can maximize their reproductive success in the face of fluctuating environmental conditions (Lack 1949; Mock & Forbes 1997), it has not been explored in the context of habitat composition and configuration to our knowledge. A few studies have examined the occurrence of brood reduction as a function of habitat type (Valkama *et al.* 2002; Shawkey *et al.* 2004), but we found none that explicitly examined the effects of habitat loss and fragmentation. This contrasts markedly with the dozens of studies that have assessed the effects of habitat fragmentation on avian reproduction through changes to predation and brood parasitism (reviewed by Stevens *et al.* 2003). Because birds can respond to environmental stochasticity more generally with modifications to both clutch size (Mazgajsk, & Reijt 2006) and brood reduction

(Hakkarainen, Koivunen & Korpimäki 1997; Valkama *et al.* 2002; Shawkey *et al.* 2004), this seems like a salient topic for additional study. In this study, saw-whet clutches did not vary with habitat composition or configuration and the rate of total nest failure was low, suggesting that brood reduction was the main mechanism by which changes in habitat composition and configuration affected saw-whet owl reproductive success.

Consistent with the pattern of brood reduction we observed and our initial predictions, the number of fledglings ultimately produced per nest was lower in landscapes with less forest cover. Many studies have linked a reduction in forest cover with lower nest success in several other cavity nesting species at both patch (Møller 1991; Riddington & Gossler 1995; Loman 2003; Mazgajsk & Reijt 2006; but see Matthysen & Adriaensen 1998) and landscape levels of analysis (Hakkarainen *et al.* 1997). Many species nesting in areas with less habitat cover and greater patch isolation must venture further afield in search of resources, which presumably reduces foraging efficiency (Bruun & Smith 2003) and provisioning rates (Luck, 2003; Suorsa *et al.*, 2003). Landscapes with less forest cover may also simply contain fewer prey items (Mills 1995; Kingston & Morris 2000) or fewer perches from which prey may be taken, both increasing the time a parent must spend foraging (Bruun & Smith 2003) and lowering provisioning rates (Hinam and St Clair unpublished data). Lower provisioning rates, in turn, have been tied to lower nest success (Ens *et al.*, 1992; Henderson & Hart, 1993; Frey-Roos, Brodmann & Reyer 1995, Maigret & Murphy,1997; but see Bruun & Smith, 2003). In support of this logic, associated work showed that male provisioning rates decreased with decreasing forest cover and increasing distance between patches and lower rates of provisioning resulted in lower reproductive success for saw-whet owls (Hinam & St. Clair unpublished data).

Conclusions

This study showed that increases in habitat loss and fragmentation were associated with higher rates of brood reduction and lower reproductive success in a cavity nesting bird, the northern saw-whet owl. As predicted, owls nesting in areas with less forest cover and more dissected landscapes raised broods that grew at a slower rate overall and had greater within-nest variation in H:L ratios, one measure of chronic stress. Nests with large broods and in which there was a greater variation in nestling stress were more likely to lose at least one chick to brood reduction and this may be a general mechanism by which reproductive success declines with habitat fragmentation in several other species. Lower reproductive success and higher incidents of brood reduction could also be directly tied to landscapes with less forest cover and smaller, more isolated nest patches.

Future studies of this nature would benefit from an examination of the within-nest variation in chick growth rate relative to landscape variation and rates of parental provisioning. Marking and following the growth trajectories of individual young would also make it possible to tie growth to nestling physiological condition. This information is particularly important for species that do not exhibit overt sibling aggression and for which rates of nest predation are low. Finally, future studies examining the fitness consequences of habitat composition and configuration should monitor the survival of the offspring post-fledging (e.g., Hakkarainen *et al.* 1997), because habitat may play an even greater role in juvenile survival once young have left the nest, altering our estimates of reproductive success. Continued detailed examination of the links between habitat changes, nestling physiology and survival are important components in improving our understanding of the effects of fragmentation on individual fitness and, ultimately, population persistence.

Table 3.1. Summary of the mean values and range for all landscape and nest patch metrics used in this study.

	Percent forest cover	Nest Patch Size (ha)	Nest patch shape index	Nest patch proximity index	Mean patch size (ha)	Patch density	Edge Density (m/ha)	Mean edge-to-edge nearest neighbour distance (m)	Normalized landscape shape index
mean	45.3	75.4	1.9	897.6	39.1	8.5	64.1	41.6	0.024
minimum	10.3	3.0	1.1	12.5	3.6	3.0	12.4	15.3	0.005
maximum	86.1	606.8	3.4	4995.1	286.7	17.0	122.5	122.5	0.060

Table 3.2. The results of a general linear model describing the relationship between the within-nest coefficient of variation of nestling heterophil:lymphocyte (H:L) ratios and landscape metrics for 45 nests between 2003 and 2005.

Dependent variable	Predictor variable	β	SE	t	P
Within nest H:L Coefficient of variation	ln(Mean patch size)	-3.09	1.496	-2.06	0.045
	Intercept	34.04	5.088	6.69	<0.001

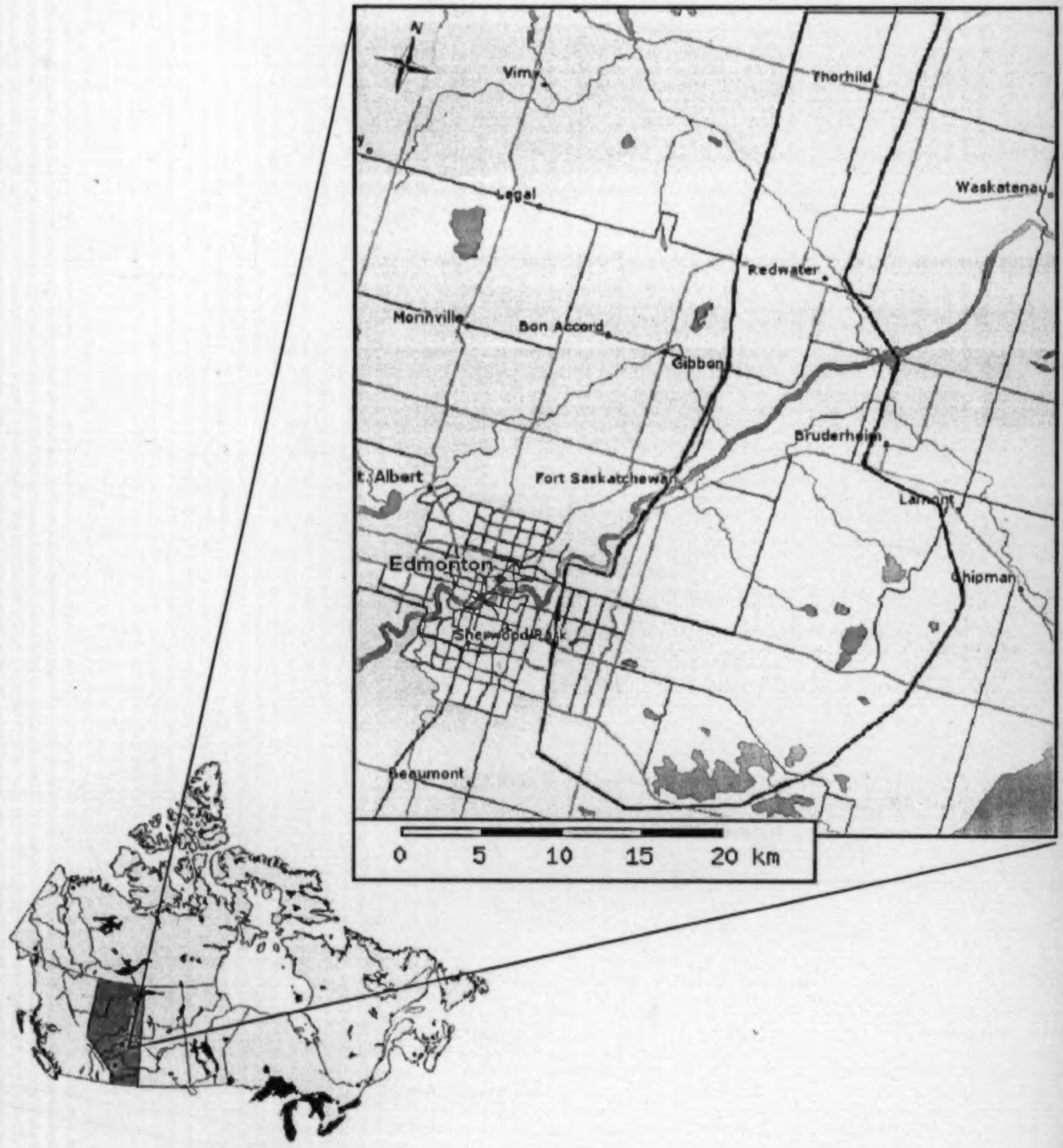
N
Vim
Thorhild
Waskatenau
Legal
Redwater
Morinville
Bon Accord
Gibbons
Bruderheim
t. Albert
Fort Saskatchewan
Lamont
Edmonton
Chipman
Sherwood Park
Beaumont
0
5
10
15
20 km

Figure 3.1. Map of the study area (highlighted), located in the aspen parkland east and north of Edmonton, Alberta, Canada (53° 32' N, 113° 33' W).

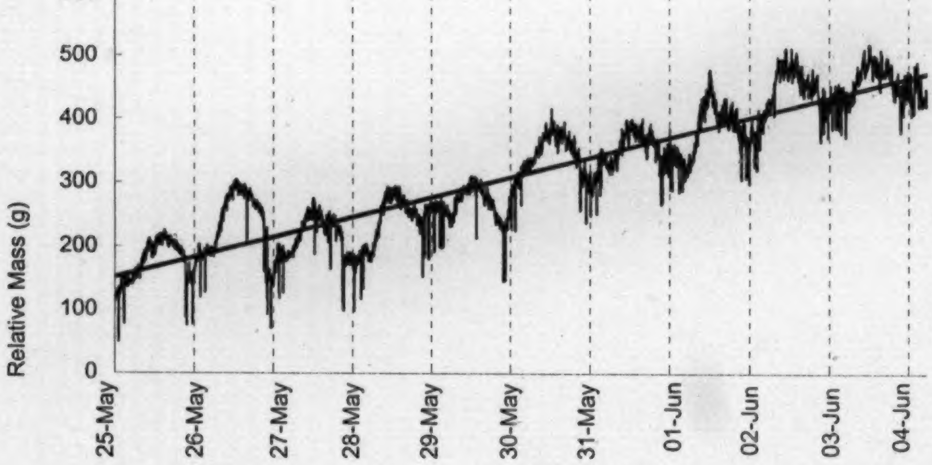

Figure 3.2. An example of the increase in relative mass of the nest contents during the first ten days after hatching showing the daily fluctuation as a result of the effect of ambient temperature on the scale. Divisions in the graph occur at 0:00h each day. The regression line denotes the overriding increasing trend associated with the growth of the nestlings.

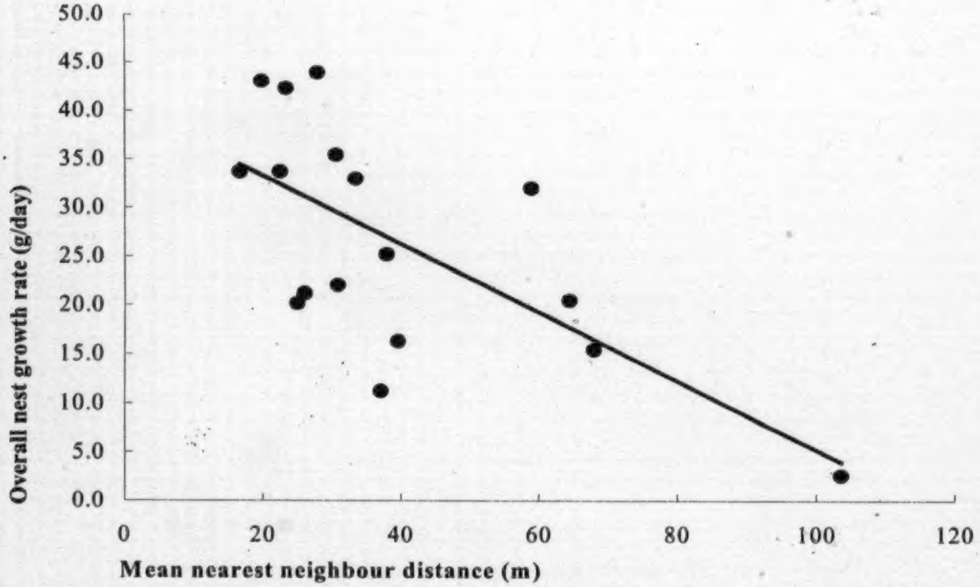

Figure 3.3. The relationship between overall nest growth rate (g/day) for 17 nests during the first 8 to 14 days of linear growth and the mean nearest neighbour distance of forest patches within 800 m nest-centred landscapes (n = 17).

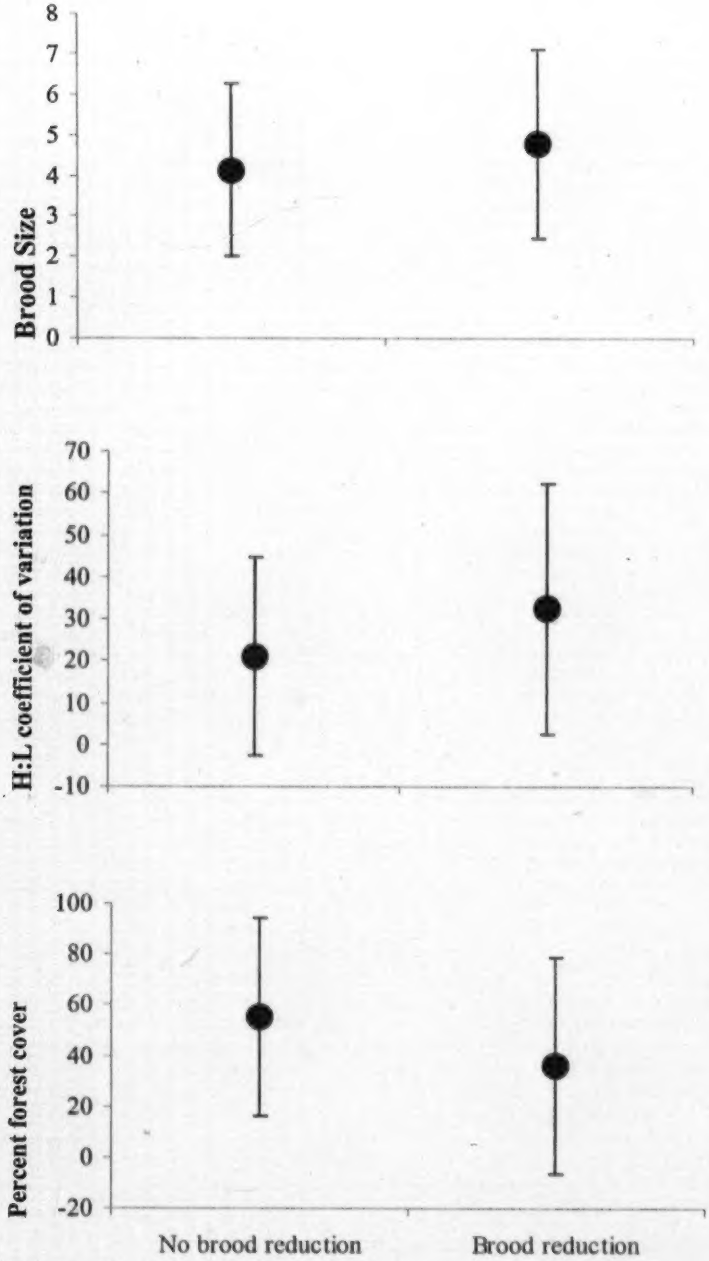

Figure 3.4. Differences in mean (± 95% confidence limits) initial brood size, H:L coefficient of variation and percent forest cover between nests in which brood reduction (loss of the youngest chick(s)) occurred (n = 17) and did not occur (n = 23).

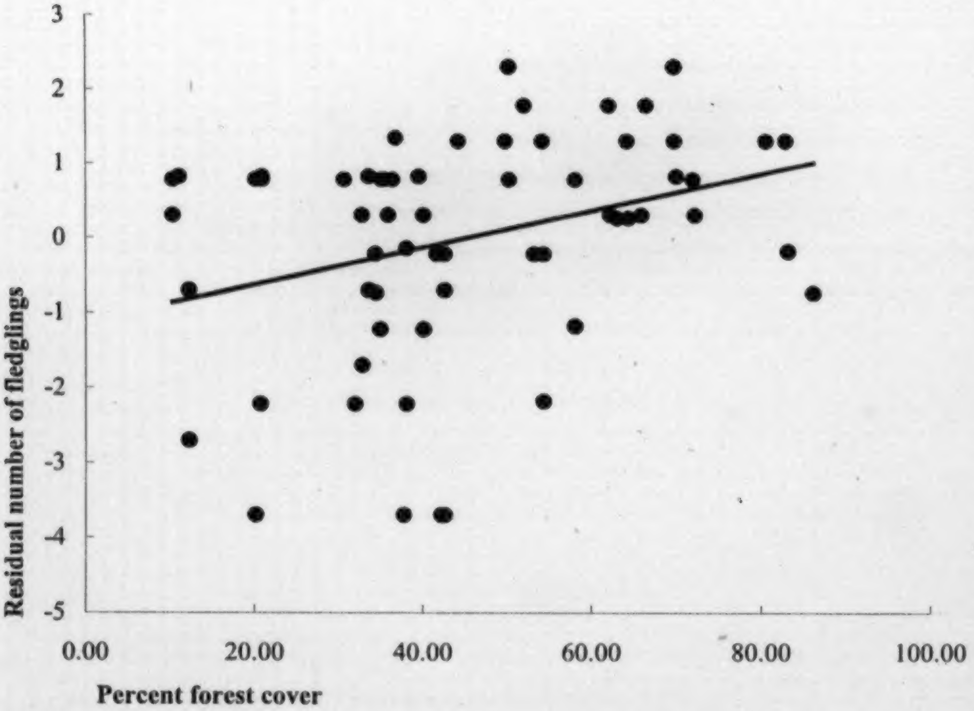

Figure 3.5. The relationship between the number of fledglings (after taking the variation due to clutch size into account) and percent forest cover within each 800 m radius nest-centred landscapes for 63 nests between 2002 and 2005. Nests in landscapes with more forest cover tended to fledge more young.

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Chapter 4 - Habitat composition and configuration affect the post-fledging behaviour, condition and survival of northern saw-whet owls

Introduction

Habitat loss and fragmentation has been linked to lower reproductive success in numerous avian species (e.g. Hoover et al. 1995; Robinson et al. 1995; see Stevens et al. 2003 for a review). The vast majority of these studies confine their investigations to the nestling stage of breeding and use overall nest survival or fledging success as measures for reproductive success (e.g. Donovan et al. 1995, Tewksbury et al. 1998; Deng and Gao 2005). However, other works have reported that post-fledging mortality can be high (e.g. Anders et al. 1997; Naef-Daenzer et al. 2001; King et al. 2006), suggesting that studies that use fledging success as an estimate of overall reproductive success may provide misleading information for estimating population demography and persistence (e.g. Naef-Daenzer et al. 2001; Kershner et al. 2004; Robinson et al. 2004).

There are several mechanisms by which habitat composition and configuration may have substantial effects on juvenile birds in the period between fledging and independence. First, a reduction in habitat amount coupled with an increase in edge and distance between remaining patches may increase barriers to the movement of dispersing individuals (Sieving et al. 1996; Desrochers and Hannon 1997; Todd 2001). Limitations to movement could curtail post-fledging exploration (Willey and vanRiper 2000; Todd 2001; Martin et al. 2006) and delay departure from the natal territory (Lens and Dhondt 1994, Matthysen and Curie 1996; Castello and Sieving 2006; but see Dzialak et al. 2006). Second, fledglings of many species select habitat during the post-fledging period that minimizes the risk of predation (Suhonen 1993; Cohen and Lindell 2004; Kershner et al. 2004; King et al. 2006). By contrast, higher rates of predation may occur in landscapes with reduced forest cover and increased fragmentation (Kotler et al. 1991; Moenting and Morris 2006) because these landscapes attract many avian predators that preferentially hunt along forest ecotones (Longland and Price 1991; Rohner and Krebs 1996; Sunde 2005). Increased predation risk may be especially important for recently fledged juveniles because they are generally less mobile, (Naef-Daenzer et al. 2001, Yakel Adams et al. 2001; Sunde 2005). Third, habitat loss and fragmentation may reduce the foraging opportunities of parents, either through lower prey availability (Sunde and Redpath, 2006) or through barriers to foraging movements (Bruun and Smith 2003; Luck, 2003; Suorsa et al., 2003). Lower provisioning rates may result in lower body condition and survival of juveniles (Frey-Roos et al. 1995; Hinam and St. Clair in preparation; but see Bruun and Smith 2003) that continue to be dependent on parental provisioning during the early post-fledging stages (e.g. Kershner et al. 2004; Sunde 2005; King et al. 2006).

In addition to these direct effects on juvenile movement, foraging success and survival, habitat loss and fragmentation may induce indirect effects on juveniles by increasing chronic stress. Stress levels, manifested both immunologically and in body condition, are known to rise in response to the frequency and perceived risk of encounters with predators (Perez-Tris et al. 2004; Navarro et al. 2004), and through chronic food shortage (Forsman and Lindell 1997; Ruiz et al. 2002). In birds, stressful circumstances generate more frequent spikes in blood corticosterone, resulting in higher ratios of white blood cells, specifically heterophils to lymphocytes, which may compromise immunity (Clinchy et al. 2002; Ruiz et al. 2002; Navarro et al. 2004; Perez-Tris et al. 2004). In addition, many avian species respond to greater perceived predation risk by maintaining lower fat reserves and thus lower body mass in order to increase maneuverability to avoid predators (Hedenström 1992; Witter and Cuthill 1993; McNamara et al. 2005). Poor body condition and greater immunological stress has been linked to delayed departure from the natal territory (Willey and vanRiper 2000), slower progression away from the nest (Ferrer 1993, but see Korpimäki and Lagerström 1988) and lower survival (Saino et al. 1997; Lochmiller and Deerenberg 2000; Christe et al. 2001; Moreno et al. 2005).

We tested both direct and indirect effects of habitat composition and configuration using the small, forest-dependent, northern saw-whet owl (*Aegolius acadicus*). Juvenile saw-whet owls fledge up to three months prior to migration (Cannings 1993) and may remain in the natal territory for nearly two months, exposing the fledglings to habitat-mediated risks and resources. The objectives of this study were to examine the relationship between variation in habitat composition and configuration on the post-fledging behaviour, physiological condition and survival of juvenile northern saw-whet owls. We predicted that juveniles occupying reduced forest cover and increased fragmentation would: 1) remain closer to the nest during the first month post-fledging and have longer post-fledging periods; 2) exhibit higher levels of chronic stress during the post-fledging period, manifested by lower body mass and higher heterophil:lymphocyte ratios, and 3) be less likely to survive the first month post-fledging.

Methods

Study species and area

We monitored juvenile post-fledging behaviour in the northern saw-whet owl between 2002 and 2005 as part of a larger study of the effects of habitat composition and configuration on the behaviour and reproductive success of this species. Young fledge at approximately 28 - 30 days old with fully developed wings, and as a result, are much more mobile at fledging than most owl species (Cannings 1993). Like many avian species, saw-whets have an extended period of post-fledging dependence where the young continue to be fed by at least one parent while transitioning to self-sufficiency (Cannings 1993). This period, which may last up to two months after leaving the nest, was the focus of this study.

Our fieldwork centered on approximately 250 nest boxes located east and north of Edmonton, Alberta, Canada (53°32'N, 113°33'W). The study area was located in the transition zone between the aspen parkland to the south and the boreal forest to the north and was characterized by patches of mature mixedwood forest (dominated by trembling aspen, *Populus tremuloides,* and white spruce, *Picea glauca*), fragmented mainly by agricultural clearing and human habitation. Forest cover ranged from 10 to 85 % in landscapes within an 800-meter radius of owl nests. The mean forest patch size in these nest-centred landscapes ranged from 4 to 286 m^2 and patches were separated (measured by edge to edge mean nearest neighbor distance) by 15 to 122 meters.

Juvenile post-fledging period, movement and survival

We monitored saw-whet nests between 2002 and 2005. Nests were checked every three to seven days from when they were discovered until fledging. Because the young hatch asynchronously, we attempted to band all the chicks in a nest just before the oldest chick fledged. Each nestling was fitted with a USFWS leg band and the oldest, which we defined as the most mobile juvenile in each nest, was equipped with a backpack PD-2P transmitter (Holohil ©). Transmitters were attached using a lightweight polyester harness that was attached over the wings, crossing over the breast and reattaching at the back of the bird (after Cannings, pers. comm.) Tagged juveniles weighed between 70.8 and 116.6 g (mean = 95.0 ± 10.2 (SD) g, n = 39) at the time of fledging, thus at 4.5 g, harnesses were near the recommended 5 % of the body weight (Caccanise and Hedin 1985) for most individuals. We did not observe any obvious detrimental effects of the transmitter on the behaviour or survival of either juvenile or adult saw-whets during the course of this study.

Fledging dates for tagged juveniles were established by regular visits to the nest every one to three days after banding and recording the date at which the individual was first located outside of the nest box. If more than one day had passed since the last nest check (to a maximum of four days), we used the average date between successive checks as the estimated date of fledging. After fledging, we relocated each individual every 1 to 8 days (mean = 5.6 days ± 1.5, n = 25). We tracked each juvenile for up to two months before recapture or until it either died or left the study area. We classified an individual as dead if the signal did not move for over one week, the carcass was found, the transmitter showed signs of trauma or if a signal disappeared within the first week of the post-fledging period when self-directed movement beyond the range of telemetry detection was unlikely (after Kershner et al. 2004). Juvenile locations were established either by re-sighting the individual or by triangulating daytime roosting sites from sequential locations (Withey et al. 2001). We relocated juveniles every one to two days when juveniles appeared to be about to leave either the nest patch or the parent's home range (located near the edge of the patch or the territory) in order to establish an accurate date of leaving. Again, if we missed the exact date of departure, we used the average date between the last two relocations (mean days between locations = 2.5 days ± 1.2 (SD)).

Locations of juveniles were used to estimate the time spent in the natal patch and the length of the post-fledging period, which was defined as the amount of time spent within the natal territory. The natal territory, in turn, was defined as a radius of 535 m from the nest; the radius of the mean home range size for males calculated for this study area (89.4 ha ± 40.2, n = 14; Hinam and St. Clair unpublished data). As an additional measure of fledging movement, we recorded the distance between the nest and each tagged juvenile after the first month post-fledging. To determine the error in our triangulated telemetry locations, we used a sub-sample of the fixes on roosting birds for which we also determined a precise location by walking in on the telemetry signal until we sighted the owl (White and Garrot 1990). We used the difference in the triangulated and actual locations to calculate mean linear error, the standard deviation of bearing error and to test for directional bias using a one-sample t-test (White and Garrot 1990).

Physiological condition

We assessed body condition for each juvenile owl both at the time of banding and again at recapture, at least 31 days and up to 48 days post-fledging (mean = 37.4 days ± 5.9). We evaluated body condition as the residual of body mass regressed against tarsus length (Ots et al. 1998) to separate the effects of condition from changes in structural size that may occur in growing young. We also assessed juvenile physiological condition using the ratio of heterophils to lymphocytes (H:L ratio) in peripheral blood samples. This ratio has been identified as a reliable measure of chronic stress in birds, increasing as stress levels increase (Gross and Siegel 1983; Ots et al. 1998; Hõrak 2002) and responding to both feeding conditions and predation risk (Ruiz et al. 2002; Navarro et al. 2004). Unlike blood corticosterone levels, H:L ratios are much less affected by acute changes in stress levels that may result from handling the birds (Gross and Siegel 1983; Vleck et al. 2000).

We collected less than one cc of blood from each juvenile by puncturing the ailar vein using a 27 ½ gauge needle and a heparinized capillary tube to collect the blood The sample was used immediately to create two whole blood smears per bird for each sampling period using a standard two-slide wedge method (Campbell 1988). Smears were stained within four months of their creation using a Wright stain, buffered using an approximate 2 % Giemsa stain solution in de-ionized water (Sigma ©) for observation at a later date. We performed a leukocyte differential on the better of the two smears for each individual both before fledging and at recapture, identifying the number of each type of white blood cell: heterophil, lymphocyte, basophil, monocyte and eosinophil in a random count of 100 white blood cells. H:L ratio was then calculated as the ratio of heterophils to lymphocytes from this differential (after Gross and Siegel 1983). Because it logically follows that H:L ratio and body condition during the post-fledging period would be directly related to individual condition at the time of fledging, we used the change in both body mass:tarsus (M:T) and H:L ratios from pre-fledging to recapture as our dependent variables.

Landscape and prey metrics

We compared the dependent variables of time spent in the nest patch, length of the post-fledging period, distance traveled from the nest, and juvenile physiological condition and survival, to a number of landscape and nest-patch level habitat composition and configuration metrics (below). These metrics were estimated from a binary GIS layer of habitat and non-habitat that we created by digitizing merged Indian remote sensing (IRS) and LANDSAT layers derived in 1998. The minimum mapping unit of the LANDSAT data was 30 m^2, however, the 4 m^2 resolution of the overlain IRS data of allowed us to identify detailed landscape features such as shelterbelts and small woodlots. We used this data to digitize a binary layer that depicted the boundaries between forest and not forest than with the LANDSAT data alone. Metrics were calculated within an 800 m radius of the nest, a value based on the mean distance traveled by foraging males in this study (Hinam and St. Clair unpublished data). We chose a larger area than that defined as the natal territory because males, which are the primary providers to the recently fledged young (Cannings 1993) foraged up to 1300 m away from the nest (Hinam, unpublished data) suggesting that a larger radius might also influence juvenile behaviour and survival in this study area.

We derived landscape metrics as independent variables using the programs ArcView 3.3 FRAGSTATS 3.3 (McGarigal and Marks 1995). We chose one habitat composition metric, three nest patch metrics and five landscape configuration metrics based on their potential importance to saw-whet behaviour and survival. We described landscape composition using the percentage of forest cover in each 800 m landscape. We described nest patch characteristics using nest patch size, nest patch shape index and nest patch proximity index. We assumed that forest cover and nest patch size both described the resources and cover available to nestlings at the landscape and patch levels respectively and that nest patch shape could describe both patch-level resource availability and possible predation risk. Nest patch proximity index (Bender et al. 2003) described how large and connected the nest patch was to the surrounding landscape and thus may affect how long a juvenile might remain near the nest after fledging. Landscape configuration was described using four metrics, patch density and mean patch size, which described the number and size of 'stepping stones' available to young moving away from the nest. Mean nearest neighbor distance described how far apart these 'stepping stones' were. Finally, edge density and the normalized landscape shape index described the complexity of the landscape and potentially the predation risk to dispersing juveniles. Juveniles moving away from the nest are more likely to encounter edges in landscapes with more convoluted patch shapes (Ewers and Didham 2006), increasing exposure to predation from edge predators such as long-eared owls (*Asio otus*) and great horned owls (*Bubo virginianus*) (Longland and Price 1991; Rohner and Krebs 1996).

A final independent variable potentially important to the behaviour, condition, and survival of juvenile saw-whet owls is prey density (Cannings 1993). Thus, we estimated relative prey density in 2003 and 2004 as the number of prints on small mammal trackplates (King and Edgar, 1977; Mabee, 1998) deployed in each nest-centered landscape. Trackplates were made of 3.7 cm diameter PVC tubing, which housed a plastic board with a two-part chemical dye in the middle and treated paper on either side to record the tracks of any small mammal moving passively through the tube. We deployed two to six lines of five trackplates in each nest-centered landscape, depending on the amount of forest cover. Trackplates were spaced 200 m apart along these lines. Half of the lines were placed along forest edges and the other half were placed in the forest interior (> 200 m from the edge). Trackplates were deployed during the late nestling season in late June and left out for 10 days (± 2 days). We then estimated relative prey density as the number of prints per trackplate for each nest.

Statistical Analysis

Statistical analyses were performed using SAS 9.1.3 (SAS Institute Inc. 2004). We modeled the effects of habitat composition, configuration and prey availability on each of the dependent variables of nest patch residence time, post fledging period, distance from the nest and change in juvenile condition using general linear and general linear mixed models where appropriate. Because changes in forest configuration are frequently related to changes in forest composition (Fahrig 1997), we tested for correlations between nest patch or landscape configuration metrics and forest cover. When variables were significantly correlated ($P < 0.05$), we regressed the patch or configuration variable against percent forest cover and used the residuals as an independent variable in the subsequent model building process (after Villard et al. 1999, Bélisle et al. 2001). Juvenile post-fledging behaviour may also be affected the yearly variations in prey abundance or weather (Wiens et al. 2006), Julian date of fledging (Arroyo et al. 2002), juvenile condition (Belthoff and Dufty 1998; Barbraud et al. 2003) and brood size at fledging (Wiens et al. 2006). To account for these potential relationships, we included year as a random effect and fledging date, brood size and fledging H:L and M:T ratios as covariates to predict the behavioural dependent variables of in length of the post-fledging period, time in natal patch and distance traveled from the nest.

We built our models with the model-building strategy outlined by Hosmer and Lemeshow (2000), which consists of identifying liberally-significant ($\alpha < 0.25$) main effects with univariate tests. Using the liberally-significant variables only, we then fit a forced entry full general linear mixed model (if random effects were included) or a general linear model (if all possible effects were fixed) and eliminating the least significant (based on $\alpha = 0.05$) variable, in each of a series of steps until significant main effects were identified. We checked for non-linear relationships graphically (James et al. 1990; Bissonetti 1999) before comparing the fit of logarithmic or quadratic terms for each variable in this model. We then added biologically plausible two-way interactions, one at a time and retained any that were significant.

We used a similar model-building approach (Hosmer and Lemeshow 2000) to examine the effects on juvenile post-fledging survival of condition at fledging, landscape, and prey variables using a multiple logistic regression. We used the Hosmer and Lemeshow (2000) statistic to establish goodness of fit and maximum rescaled r^2 to describe the predictive power of the final model (Allison 1999).

Results

Post-fledging period and behaviour

One juvenile from each of 46 nests was radio tagged between 2002 and 2005. Of those 46 juveniles, 14 died during the first month post-fledging and the fates of an additional seven are unknown. We tracked 25 juveniles for a period equal to or greater than one month (mean = 40.3 days ± 8.3(SD); n = 25) and we recaptured 19 fledglings. Telemetry error was calculated using 37 tagged, roosting owls that were between 26 and

1484 m away from the observers. Mean linear error was 62.8 m (± 52.6, n = 38). Bearing error was unbiased (mean difference between actual and estimated bearings = 0.39°; t = 0.289, P = 0.774, df = 77), and the standard deviation of errors was 22.5°.

Fledglings were relocated an average of every 5.6 days (± 1.5; n = 25). Juveniles spent on average 28.2 days (± 8.02 SD, n = 18) in the natal patch before crossing into another habitat patch. Variation among nestlings in the duration of time spent in the natal patch was not significantly explained by any of the landscape or prey metrics examined in this study ($F_{1,16} < 1.16$, P > 0.222 for all nest patch and landscape metrics, $F_{1,12} = 1.15$, P = 0.304 for print density). The time spent in the natal patch was also not significantly related to fledging date ($F_{1,16} = 0.48$; P = 0.498), brood size ($F_{1,16} = 1.79$; P = 0.200) or immunological condition at fledging ($F_{1,14} = 0.48$; P = 0.515). However, the total length of the post-fledging period, measured as the length of time in the natal territory (as opposed to patch) varied with habitat configuration. Juveniles remained within the natal territory between 18 and 49 days (mean = 31.9 days ± 7.7; n = 19) and the length of the post-fledging period increased logarithmically in landscapes with larger distances between habitat patches ($F_{1,16} = 8.73$; P = 0.009; Fig. 4.1) and more complex habitat edges ($F_{1,16} = 10.32$; P = 0.005; Fig.4.1). These two variables accounted for 45 % of the variation in the post-fledging period data ($F_{2,16} = 6.79$; P = 0.007; Fig. 4.1).

At approximately one month post-fledging, juveniles were relocated between 62.5 and 1453.4 m from the nest (mean = 458.8 m ± 326.5; n = 25). The distance traveled from the nest at this age did not vary significantly with the number of times the juvenile had been relocated ($F_{1,23} = 0.297$; $P = 0.591$; $r^2 = 0.01$). However, juveniles were found closer to the nest in landscapes with more complex habitat edges (high landscape shape index) and juvenile distance from the nest increased logarithmically in more contiguous landscapes with simpler edges (low landscape shape index; $F_{1,23} = 9.50$; $P = 0.005$; $r^2 = 0.29$; Fig. 4.2).

Changes in physiological condition

We assessed changes in heterophils:lymphocyte (H:L) ratio and residual body massbetween fledging and recapture for 16 and 15 juveniles respectively. Juveniles had been out of their nests for 31 to 48 days before recapture (mean = 37.4 days ± 5.9). However, there was no relationship between either the change in H:L or residual body mass and the number of days between the first and second sample ($F_{1,14} = 0.003$; $P = 0.995$ and $F_{1,13} < 0.001$; $P = 0.984$ respectively). Juvenile tarsus length increased only slightly during the post-fledging period (mean increase = 0.57 mm ± 0.73), suggesting that the bulk of saw-whet structural growth occurred during the nestling stage. Changes in mass, however varied widely from positive (max = +10.8 g) to negative (min = -18.2 g). Thus, the variation in juvenile residual body mass was driven primarily by changes in body mass. Contrary to predictions, juveniles tended to lose weight during the post-fledging period in landscapes with greater forest cover and gain weight in areas with less forest cover ($F_{1,13} = 6.48$, $P = 0.024$; $r^2 = 0.33$ Fig. 4.3).

Similar to the body condition metric, change in H:L ratio in juveniles ranged from an increase in chronic stress (max = + 0.78) to a decrease (min = -0.62; mean = -0.14 ± 0.46; n = 16) during the post-fledging period. As predicted, juveniles in areas with higher forest cover showed a greater reduction in chronic stress, as indicated by the change in H:L ratios, whereas, juveniles in landscapes with less forest cover exhibited an increase in chronic stress levels ($F_{1,14} = 14.10$; $P = 0.002$; $r^2 = 0.50$; Fig.4.4) during the post-fledging period. This positive relationship with forest cover explained just over 50% of the variation in the data.

Juvenile Survival

We were able to record the fate of 38 of the 46 radio-tagged juveniles. Twenty-four survived the first month post-fledging and 14 did not. Of the 14 that died, three starved and 11 were believed to have been depredated. Three individuals (1 dead, 2 alive) could not be used in the modeling process because we had not collected physiological data for them. Juveniles that survived the first month post-fledging exhibited lower H:L ratios at the time of fledging (Wald = -6.78; df = 1; P = 0.011; Fig. 4.5) and were found in landscapes with a greater amount of forest cover (Wald = 4.17; df = 1; P = 0.041; Fig. 4.5). These two variables produced a significant logistic regression model ($\chi^2 = 6.51$; df = 2; P = 0.038; Fig. 4.5). The Hosmer and Lemeshow (2000) statistic and the maximum rescaled r^2 indicated that this model fit reasonably well and explained 33% of the variation in the data (Hosmer and Lemeshow goodness of fit statistic = 8.49; P = 0.291; df = 7). There was no significant interaction between the effects of forest cover and fledging H:L ratios on juvenile survival (Wald = 1.32; df = 1; P = 0.250).

Discussion

The period between fledging and dispersal is a time of transition for juvenile birds. During this time they are dependent on their parents for food and are often unable to fly for long distances, which may cause an increase in predation risk (Anders et al. 1998). It may be for this reason that recently fledged juveniles typically seek habitat to reduce the risk of predation during forays away from the nest (Suhonen 1993; Anders et al. 1998; Cohen and Lindell 2004; King et al 2006). For forest birds, landscapes with forest patches that are widely scattered and that have complex habitat edges relative to their size may present more risky areas for recently fledged birds (Lima and Dill 1990; Todd and Cowie 1990; Suhonen 1993) and thus may curtail juvenile post-fledging movements (Todd 2001; Martin et al. 2006) and prolong post-fledging periods (Lens and Dhondt 1994; Sieving et al. 1996; Todd 2001).

In our study, juvenile northern saw-whet owls that fledged into landscapes with more complex forest edges remained closer to the nest during the first month post-fledging. Complex habitat edges and larger distances between habitat patches also resulted in juveniles remaining in the natal territory for up to a month longer than fledglings in more continuous habitat. Relatively little work has been done on juvenile post-fledging behaviour in the context of habitat composition and configuration. However, similar apparent reductions in post-fledging movements (King and Belthoff 2001; Todd 2001; Dzialak et al. 2006; Martin et al. 2006) and longer post-fledging periods (Lens and Dhondt 1994; but see Dzialak et al. 2006) have been recorded in both passerines and raptors. Moreover, predation risk has been suggested as a driving factor in the post-fledging behaviour for many species (Bélisle and Desrochers 2002; Harris and Reed 2002). For our fledging saw-whet owls, the pattern to remain closer to the nest in landscapes with more complex forest edges and greater distances between habitat patches functions may be to avoid exposure to predation from great horned owls and long-eared owls, which athough have been found to breed in landscapes with moderate amounts of forest cover and edge (Marks et al. 1994; Hinam 2001; Grossman 2003), have been found to hunt along forest edges and in open habitats (Longland and Price 1991; Rohner and Krebs 1996) and which are frequently observed in our study area (H. Hinam, personal observation).

Alternatively, although juvenile post-fledging behaviour and condition was not directly affected by prey density as measured in this study, it may have been affected indirectly by landscape characteristics affecting prey availability. During this period of transition to independence, juveniles also select for habitats with greater resources (Kershner et al. 2004). Landscapes with more complex edges may have higher densities of some small mammal species (Bayne and Hobson 1998; Manson et al. 1999), attracting juveniles during the post-fledging period and potentially lengthening the time to dispersal. Indeed, saw-whet owls occurring in parts of this study area have been associated with complex forested landscapes, possibly because of increased opportunities for hunting (Grossman 2003). However, juveniles of many avian species have been found to disperse from the natal territory sooner when in better condition, resulting from more food (e.g. Wiley and vanRiper 2000; Arroyo et al. 2002; Barbraud et al. 2003). Thus if landscapes with more complex edges offered higher prey densities, we would have expected shorter post-fledging periods in these areas.

The physiological condition of juveniles during the period between fledging and independence was also affected by variation in landscape-level habitat. However, the effects of habitat composition on body condition and immunological condition were in opposing directions and not, at first appearance, consistent. Many juveniles lost body mass once corrected for body size from just prior to fledging until recapture over one month later, a common pattern in birds as they approach fledging and independence (Ricklefs 1968; Huin and Prince 2000). Loss of mass post-fledging may aid in increasing mobility and thus potentially improve the ability of fledglings to avoid predators (Hedenström 1992; Witter and Cuthill 1993) and eventually forage for themselves. However, in our study, the individuals that gained mass during the post-fledging period were found in landscapes with low forest cover, contrary to what would be expected if reductions in mass result from an increase in perceived predation risk (McNamara et al. 2005). This opposing pattern may be a function of the both prey availability in these landscapes and typical anti-predator behaviour of saw-whet owls, which consists of perching, immobile in a concealed location (Sealy and Hobson 1987). Landscapes with lower forest cover may offer fewer refuges from predators (Lima and Dill 1990; Todd and Cowie 1990; Suhonen 1993) for saw-whet owls from predators such as great horned owls and long-eared owls which have been observed hunting in open areas and along forest edges (Longland and Price 1991; Rohner and Krebs 1996). Many birds stop feeding in the presence of a predator (Pravosudov and Grubb 1998), especially when anti-predator behaviour includes a concealment posture. As a result, individuals may increase feeding intensity between encounters to guard against starvation, resulting in greater mass increase over time (Houston and McNamara 1993; McNamara et al. 2005). Interestingly, a similar pattern of higher body masses was also observed in adults of this species foraging in landscapes with greater amounts of edge (Hinam and St. Clair unpublished data).

If mass gain is indeed a response to higher predation risk, then this trend may be more consistent than it first appeared. We also observed an increase in chronic stress in juveniles post-fledging in landscapes with with less forest cover. During the post-fledging period, most juveniles showed a reduction in chronic stress levels, as indicated by decrease in blood H:L ratios, potentially as a result of relaxed sibling competition associated with juveniles leaving the close confines of the nest. However, this general trend was moderated by habitat. As predicted, juveniles from landscapes with greater forest cover exhibited declines in H:L ratios during the post-fledging period, presumably because they experienced less chronic stress, either through reduced predator pressure or greater prey availability. Similar results occurred for adult male northern saw-whet owls in this study area (Hinam and St. Clair, in review) and other species (Ruiz et al. 2002). This pattern is logical if landscapes with less forest are perceived as more dangerous either because they offer fewer places for juveniles to hide from predators or because actual encounters with predators increase there (Andreanssen and Ims 1998), both of which could result in increased spikes in blood corticosterone (Clinchy et al. 2002; Navarro et al. 2004).

Both immunocompetence and variation in habitat composition affected the probability with which juveniles survived the first month post-fledging. Specifically, fledgling saw-whet owls were more likely to survive this first month if they fledged with lower blood H:L ratios and into landscapes with higher percentages of forest cover. This result is consistent with many studies that have linked poor immunocompetence with lower survival (Lochmiller and Deerenberg 2000; Christe et al. 2001; Moreno et al. 2005). Juveniles that leave the nest with higher levels of chronic stress may be at a disadvantage in their transition to independence mainly because they may be more susceptible to predation (Møller and Erritozøe 2000; Adams et al. 2006), pathogens and parasites (Ots et al. 1998). Because predators often preferentially choose more vulnerable prey (Cresswell and Quinn 2004), juveniles with poor immunocompetence may be more vulnerable through changes in their escape behaviour (Martin et al. 2006), or by increasing their detectability through higher begging rates (Adams et al. 2006). The concealment anti-predation strategy of saw-whet owls may increase their dependency on parental provisioning resulting in higher body weights (above) as well as higher predation rates mediated by begging behaviour. Predation rates may be further increased in habitats with lower forest cover because they do not provide sufficient refugia from predators (Andreanssen and Ims 1998). Landscapes with lower forest cover may also offer fewer resources to transitioning young , either directly through less forest area to exploit themselves or indirectly by reducing the provisioning rates of parents during the initial post-fledging stages (Luck, 2003; Suorsa et al., 2003; Tremblay et al., 2005; but see Nour et al., 1998), resulting in a greater chance of starvation. Adult provisioning rates earlier in the nestling stage have been shown in this study area to be lower in landscapes with less forest cover (Hinam and St. Clair, unpublished data).

In sum, variation in both habitat composition and configuration was associated with juvenile behaviour, condition and survival during the post-fledging period for saw-whet owls in a fragmented agricultural landscape. Juveniles in landscapes with more complex edges and a greater distance between habitat patches exhibited constrained post-fledging movements and remained longer in the natal territory. Low forest cover was related to higher levels of chronic stress and higher body mass in juveniles and reduced juvenile survival during the first month post-fledging. For saw-whet owls, habitat loss and fragmentation may have resulted in increased predation risk, influencing the characteristics of the post-fledging period as suggested by several other species (e.g. Naef-Daenzer et al. 2001; Kershner et al. 2004; King et al. 2006). However, other studies have suggested that juvenile survival and behaviour is mainly related to prey availability (Morton 1991; Anders et al. 1998). In this study, it is likely that both prey availability and predation risk act in concert to affect juvenile behaviour and condition. More work would be needed to know if the apparent unimportance of prey density in this study is a genuine reflection of its relevance to post-fledging survival or if it was simply inappropriately measured. Regardless of the importance of prey, this study suggests that higher levels of chronic physiological stress are associated with lower individual survival and hence, parental fitness. What is uncertain is how constrained post-fledging movements, and longer post-fledging periods relate to the success of juveniles in breeding seasons to come. Although it would be difficult to achieve in saw-whet owls, which have low natal site fidelity (Cannings 1987), studies that record the subsequent breeding success of juveniles produced in habitats of different types would provide important additional information about how habitat composition and configuration affect individual fitness and, ultimately, population persistence.

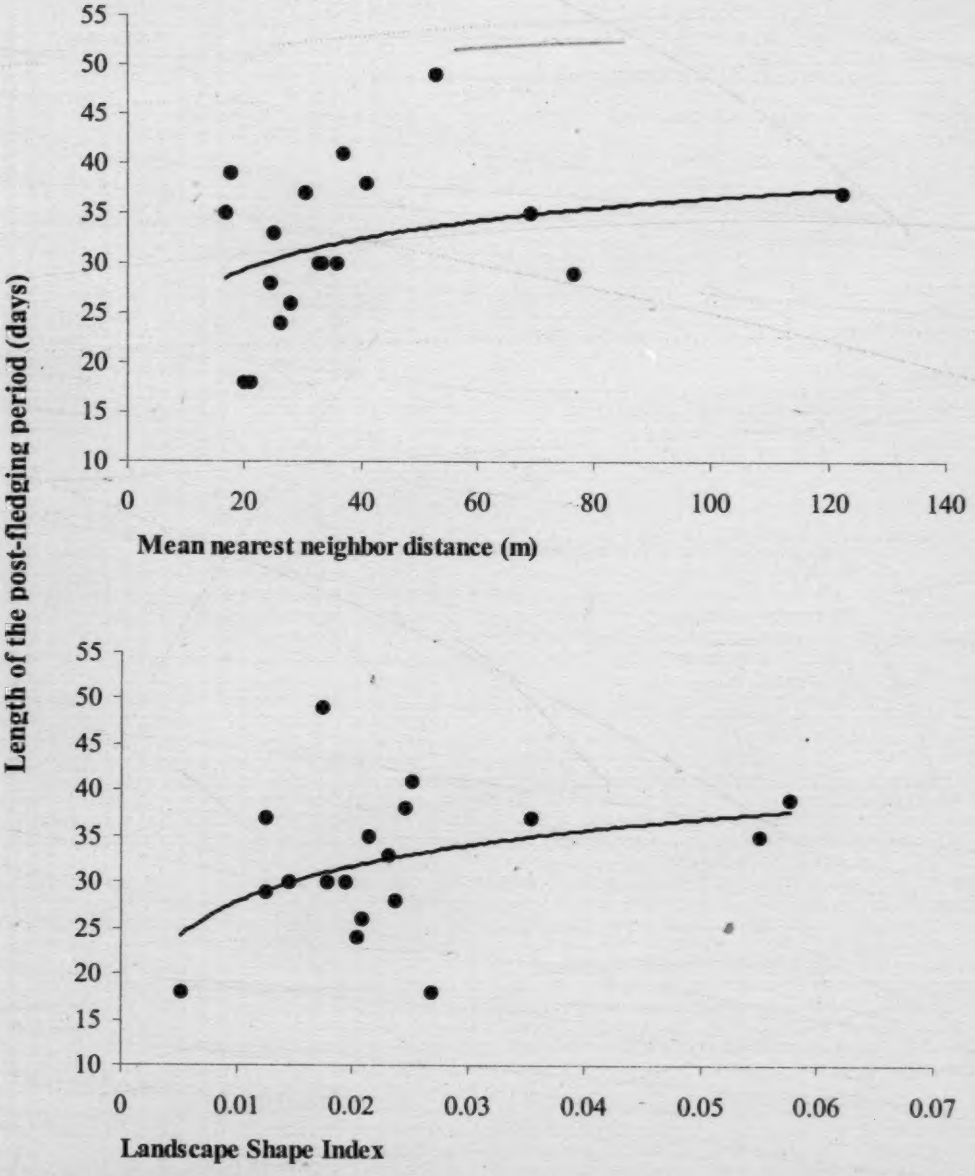

Figure 4.1. The relationship between the number of days a fledgling spent within its parent's home range (post-fledging period) for 19 individual juveniles and increasing mean edge-to-edge nearest neighbour distance (metres) and increasing landscape complexity (higher landscape shape indices).

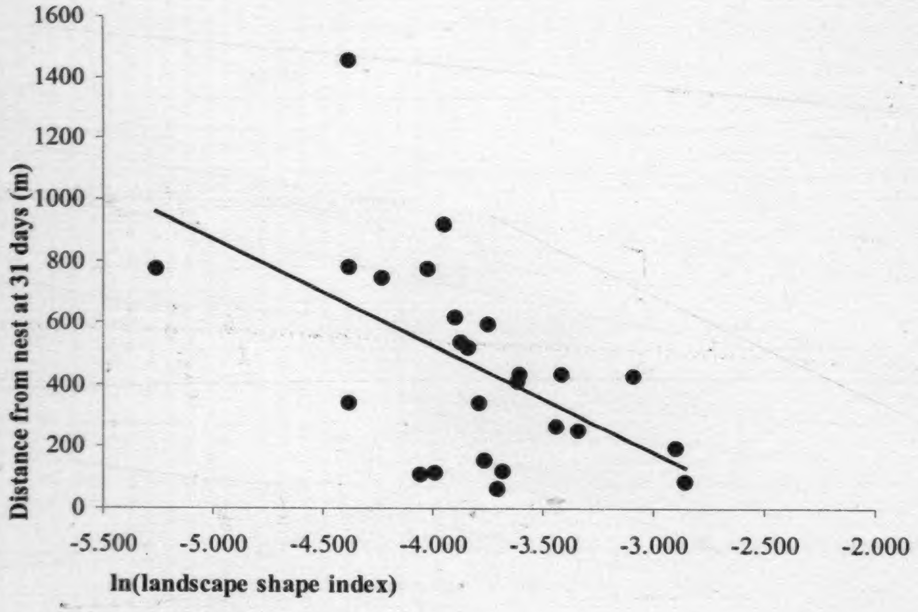

Figure 4.2. The relationship between the distance from the nest that juveniles were relocated after the first month post-fledging (n = 24) and the natural log increase in landscape shape index (increasing edge complexity) for habitat within 800 m of the nest.

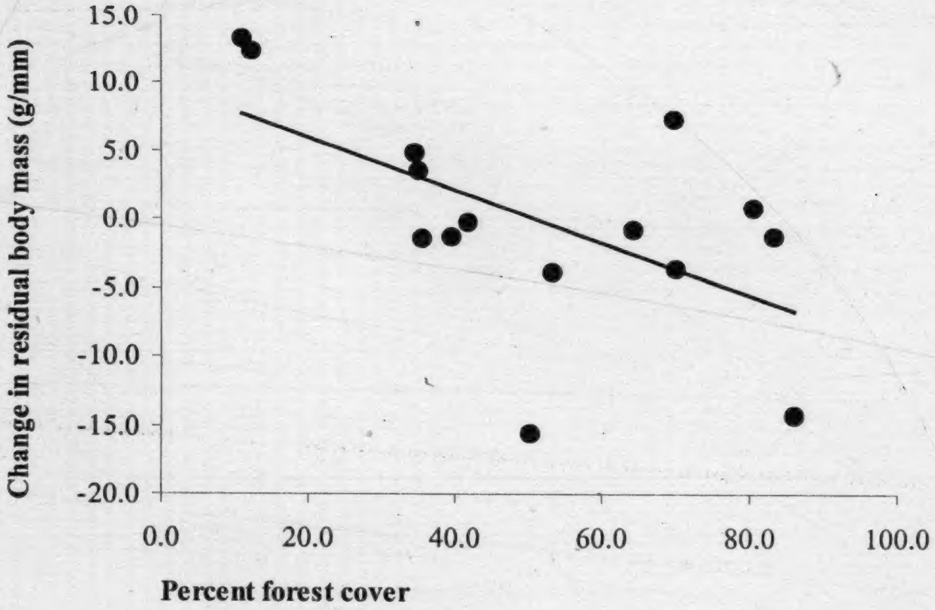

Figure 4.3. The relationship between the change residual body mass of 15 juveniles during the post-fledging period and increasing forest cover within 800-m radius nest-centred landscapes.

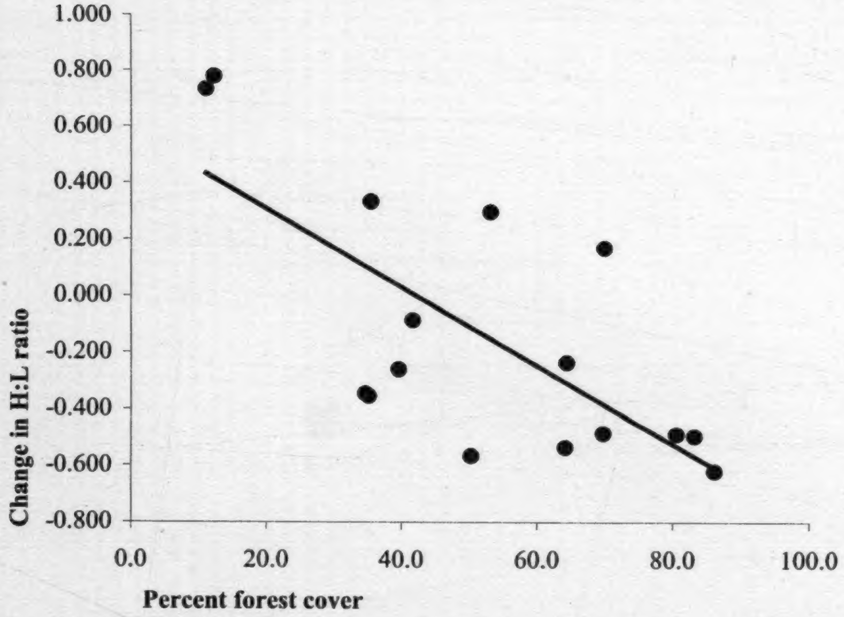

Figure 4.4. The relationship between the change in the ratio of heterophils to lymphocytes (H:L ratio) in 17 juveniles from just prior to fledging until up to 48 days post-fledging and the percent forest cover within 800 m of the nest. Lower H:L ratios describe chicks in better physiological condition.

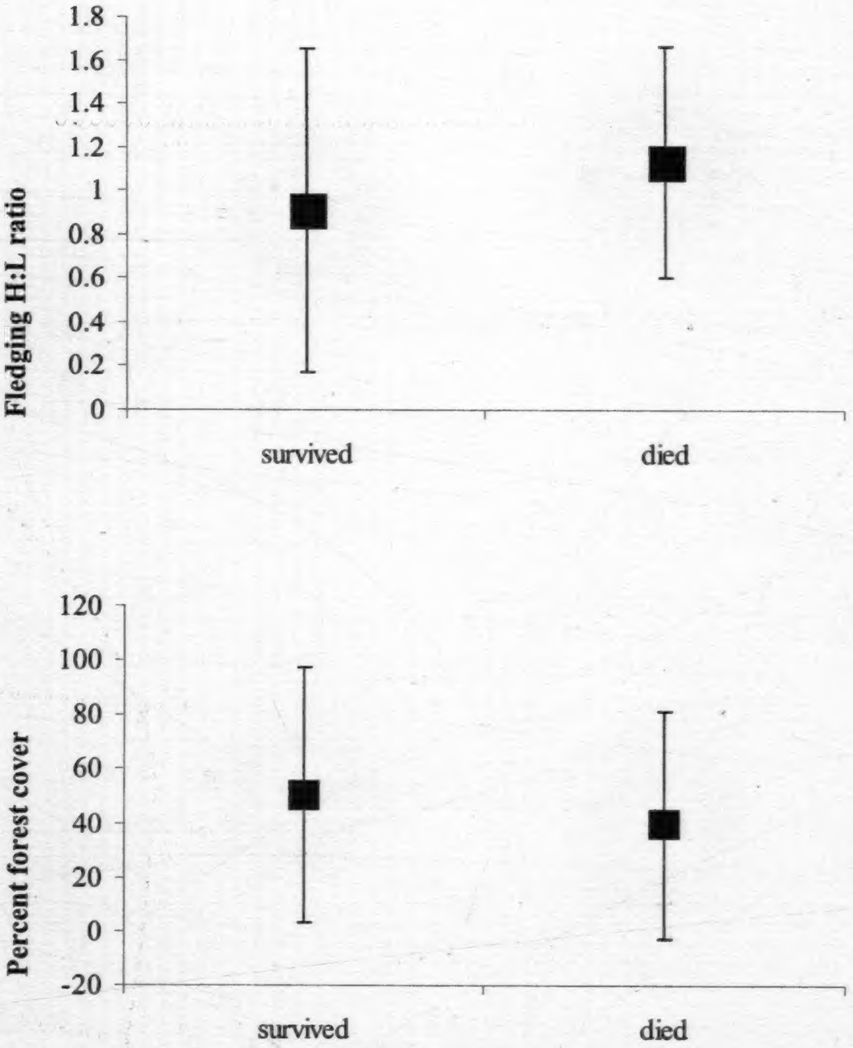

Figure 4.5. Mean fledgling heterophil:lymphocyte ratio and mean percent forest cover (± 95% confidence limits) for juvenile northern saw-whet owls that survived the first month post fledging (n = 22) and those that died during the first month out of the nest (n = 14).

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Chapter 5 – General Discussion

Habitat loss and fragmentation had a significant effect on the behaviour and physiological condition of both adult and juvenile northern saw-whet owls. These effects translated to lower survival for juveniles and lower reproductive success for adults, indicating that habitat characteristics have substantial fitness implications for individuals and the potential to limit population viability. Here I review these effects by comparing them for juvenile and adult owls. I conclude by synthesizing these results, relating them to the literature and suggesting avenues of profitable future research.

Although both adult male foraging and juvenile post-fledging behaviour were associated with landscape-level habitat variation, male foraging was affected by both composition and configuration, whereas, juveniles were affected by configuration only. Males spent longer at a perch in areas with less forest cover and foraged longer in more isolated patches and thus maintained smaller home ranges in landscapes with little forest cover and large amounts of forest edge. Similarly, juveniles remained closer to the nest post-fledging and thus remained in the natal territory longer in landscapes with more complex forest edges relative to area. However, there was no relationship between juvenile post-fledging periods and the amount of forest cover. In both cases, reductions in movement under lower or more fragmented forest cover likely reflected a behavioural adaptation to a perception of increased predation risk in these habitats (Desroches and Hannon 1997; Bélisle and Desrochers 2002; Harris and Reed 2002).

Differences between adult males and juveniles may have reflected variation in behavioural motivation (Belisle 2005).

There are several reasons that predation is likely the main factor influencing movement behaviour of juveniles. During the post-fledging period, juveniles remain dependent on adult provisioning for much of the time (Cannings 1993; Anders et al. 1998) and thus do not need to find their own food. Instead, juveniles of many species choose habitat in order to reduce the risk of predation (Suhonen 1993; Anders et al. 1998; Cohen and Lindell 2004; King et al 2006) while they await parental deliveries. For young saw-whets, edges can be risky due to an often higher concentration of avian predators (Andreassen and Ims 1998). Thus, in landscapes with complex forest edges, juveniles may be forced to curtail exploratory movements (King and Belthoff 2001; Todd 2001; Dzialak et al. 2006; Martin et al. 2006) and remain in the natal territory longer before suddenly dispersing long distances (Lens and Dhondt 1994; but see Dzialak et al. 2006).

Predation risk also appears to influence male foraging decisions, as evidenced by their reluctance to move out more isolated forest patches and smaller home ranges in landscapes with large amounts of forest edge. Individuals of other species breeding in landscapes with less forest cover and greater fragmentation also exhibit more centralized movements and a greater reluctance to cross gaps (Bayne and Hobson, 2001; Fraser and Stutchbury, 2004). However, male movement behaviour is also motivated by the demands of foraging and provisioning young (Elchuk and Wiebe

2003). Thus, if predation risk is relaxed in areas with greater forest cover, this motivation likely drove the increase in home range size in saw-whet males in search of more resources (Elchuk and Wiebe 2003) to a maximum size, likely dictated by the time costs and energetic constraints of provisioning a central place (Krebs 1980).

Due to the low natal philopatry exhibited by saw-whet owls (Cannings 1987; Marks and Doremus 2000), it is unclear how contracted post-fledging movements and longer post-fledging periods affect fitness over the longer term. In some species, earlier juvenile dispersal appears to be linked with better chances of settling in a territory and subsequently breeding (Nilsson 1989; Matthysen and Curie 1996). Martin et al. (2006) suggested that truncated exploratory movements, resulting from habitat fragmentation, might reduce an individual's ability to contend with sudden changes in habitat quality. The links between habitat variation and movement behaviour in males were more readily apparent. In this study, longer perch times occurred in landscapes with less forest cover and more isolated patches. This change in habitat-mediated foraging resulted in lower provisioning rates to the nest; a direct fitness consequence. The lower provisioning rates I observed resulted in fewer young fledged and this result has also occurred in many other species (Ens et al. 1992; Henderson and Hart 1993; Frey-Roos et al. 1995, Maigret and Murphy 1997; but see Bruun and Smith 2003). Reduced provisioning rates caused concomitant reductions in nestling survival, as observed in several other avian species (Hinsley et al. 1999; Hakkarainen et al. 2003; Loman 2003; Mazgajsk and Reijt 2006).

In addition to the effects of lower provisioning rates, owls nesting in more fragmented areas may have exhibited lower reproductive success because they also produced smaller clutches (Mazgajsk and Reijt 2006). However, I found no relationship between clutch size in saw-whets and habitat, making it likely that the reduction in the number of young fledged stemmed instead from losses during the nestling stage. Northern saw-whet owls are asynchronous hatchers (Cannings 1993), resulting in competitive asymmetries among nestlings, which may be exacerbated by lower provisioning rates due to habitat loss and fragmentation (Kitayski et al. 1999). These asymmetries should be manifested through variation in behaviour and physiological condition during the nestling period and beyond.

One change in behaviour that is likely to result from the food stress of young experiencing lower provisioning rates is a higher incidence of antagonistic behaviour among nestlings (Mock and Parker 1997). Sibling aggression may result in chronic stress (Tarlow et al. 2001; Blanco et al. 2006), and may be manifested by higher heterophil-lymphocyte ratios (H:L) resulting in immunosuppression (Gross and Siegel, 1983). Because stress levels are often negatively correlated with the dominance hierarchy within a nest (Schwabl, 1999; Tarlow et al., 2001; Love et al., 2003), lower provisioning rates as a result of habitat loss and fragmentation may trigger brood reduction through the loss of the more chronically stressed young (*sensu* Lack 1947, Mock and Parker 1997). Indeed, examination of a larger sample of nests in which I could establish whether brood reduction did or did not occur (chapter 3) revealed that young were more likely to be lost to brood reduction in nests where the within-nest variation in H:L ratios were the greatest. The probability of brood reduction occurring also increased in landscapes with lower forest cover. Thus, the lower reproductive success of owls living in habitats with little forest cover may have been an adaptive response to conditions that provided fewer foraging opportunities and greater variability in the condition of their offspring, resulting in more nestlings lost to brood reduction.

The effects of habitat loss and its relationship to nestling condition had a continued negative effect on reproductive success by lowering juvenile survival post-fledging. Poor immunocompetence has been linked to lower juvenile survival in a number of species (Lochmiller and Deerenberg 2000; Christe et al. 2001; Moreno et al. 2005). Indeed, juveniles in this study were more likely to perish during their first month post-fledging in landscapes with lower forest cover and if they fledged with higher H:L ratios. This result may have important ramifications for estimates of population viability. Many studies of reproductive success neglect to monitor survival of nestlings post-fledging (e.g. Donovan et al. 1995, Tewksbury et al. 1998; Deng and Gao 2005). Ignoring this period may be particularly misleading in species, like this one, in which habitat loss may affect juvenile survival both directly, through lower nestling survival, and indirectly, through poorer fledging condition (e.g. Naef-Daenzer et al. 2001; Kershner et al. 2004; Robinson et al. 2004).

In addition to their effects during the pre- and post-fledging period, habitat loss and fragmentation may also affect the future fitness of individuals through negative and lasting effects on physiological and immunological condition. Both adult male and juvenile saw-whet owls responded to landscapes with lower forest cover with higher ratios of heterophils to lymphocytes. As with the patterns observed with individual behaviour, it is likely that these trends were a function of predation risk. Landscapes with less forest cover may be perceived as more dangerous, offering fewer refuges from avian predators (Andreassen and Ims 1998). Spikes in blood corticosterone levels have been observed in a number of species in response to and increase in perceived predation risk (Clinchy et al. 2002; Navarro et al. 2004), resulting over time in immunosuppression and thus higher H:L ratios (Gross and Siegel 1983). Immune suppression in birds has been linked to lower reproductive success (Moreno et al. 1998; Hanssen et al. 2003), higher parasite loads and risk of disease (Saino et al. 1997; Christe et al. 1998) and higher mortality rates (Christe et al. 1998), which may persist over the long term and may affect genetic diversity and population survival over time (Fairbrother et al. 2004).

The effects of habitat loss and fragmentation on body mass was consistent between adults and juveniles, however, the trends appear counterintuitive at first glance. Many avian species lose body mass relative to size in the presence a predator in an effort to improve manoeuvrability for escape (Macleod et al. 2005; McNamara et al. 2005). In this study however, both adult and juvenile saw-whets gained weight in landscapes with less forest cover and more complex edges. If these landscapes are indeed more risky (Andreassen and Ims 1998), then this observed pattern seems at first, unexpected. Mass loss as a response to increased predator risk may not be an adaptive strategy for saw-whet owls because the primary anti-predator behaviour of both adult and juvenile owls is not flight, but to remain stationary in a 'concealed' pose among dense vegetation (Sealy and Hobson 1987). Instead, the higher mass of owls in fragmented habitats may occur because birds are unable to forage when subject to predation risk (Pravosudov and Grubb 1998), thus it may be advantageous for individuals to maintain higher body masses to offset starvation instead of maintaining manoeuvrability (Houston and McNamara 1993; McNamara et al. 2005). Although, because of its tendency to fluctuate seasonally and even daily, body mass may not be a reliable indicator of long-term fitness (Ots et al. 1998). However, for provisioning males, maintaining a higher body mass may increase the physiological costs of provisioning young through increased wing loading (Freed 1981; Norberg 1981), potentially impairing flight ability (Kullberg et al. 2002) and reducing provisioning rate, and thus reproductive success.

Conclusions

Habitat loss and fragmentation are among the most pervasive causes of biodiversity loss through population declines (see Fahrig 2003; Cushman 2006; Ewers and Didham 2006; for reviews). However, the mechanisms underlying these patterns are complex and inaccurate or untested assumptions may have important implication for estimates of population viability (Anthony and Blumstein 2000). Incorporating studies of individual behaviour and fitness into conservation plans can improve population modelling, especially when such studies target behavioural and physiological variables that may affect vital rates, such as reproductive success and survival (Caro 1999; Wikelski and Cooke 2006). Unfortunately, the logistic constraints associated with examining the behaviour of free-ranging animals and the often long time frames needed to collect sufficient long-term data (Sutherland 1998; Hames et al. 2001) promote a focus on organisms with relatively small home ranges and patch-level questions. This is unfortunate because most problems of landscape fragmentation occur at the spatial extent of landscapes (Yahner and Mahan 1997; McGarigal and Cushman 2002).

This detailed study of northern saw-whet owl behaviour and reproductive success in the context of landscape level variation in habitat composition and configuration has demonstrated measurable links between habitat loss and fragmentation and lower provisioning rates by male parents. Lower provisioning rates were, in turn, linked to lower reproductive success. Lower reproductive success was indirectly and directly related to brood reduction, which may have been mediated through increased within-nest disparity in immunological condition. Finally, increased habitat loss and fragmentation resulted in curtailed post fledging movements, higher physiological stress for both adults and juveniles and lower juvenile survival. Lower juvenile survival was demonstrated directly during the pre- and post-fledging period and may extend into subsequent life stages through the lower condition of juveniles under these habitat conditions. In sum, the study has shown that habitat composition and configuration affect several aspects of the movement behaviour, condition, and reproductive success of owls, providing a mechanistic basis for the wider-spread assertion that habitat loss and fragmentation reduce the viability of natural populations (e.g. Fahrig 2003; Ewers and Didham 2006).

Despite the effects I have demonstrated in this study, much work remains to be done. My interpretations are limited by small sample sizes and the inability to determine the effects of higher stress levels and curtailed post-fledging movements on long-term individual fitness. The next step is to examine these questions in the context of organisms that can be tracked for several years to determine if the effects of habitat loss and fragmentation on individual fitness is cumulative over time. As the demand by those making conservation decisions for data on the causal mechanisms of species declines increases (Wikelski and Cooke 2006) and focus continues to shift to recognize the importance of individual fitness on ecosystem functioning (Yahner and Mahan 1997; Anthony and Blumstein 2000; Marzluff and Ewing 2001), such long-term studies will be very important to explaining, predicting and potentially mitigating, the observed relationships among habitat loss, habitat fragmentation, and biodiversity.

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